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THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.
Clerk of Publications . . . G. B. STRATTON, M.B.E.

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ON THE GROWTH OF THE BROWN TROUT OF LLYN TEGID

BY

J. N. BALL AND J. W. JONES

Department of Zoology, University of Liverpool

[Accepted 12th May 1959]

(With 3 plates and 15 figures in the text)

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I. INTRODUCTION

Llyn Tegid (Bala Lake), the largest Welsh lake, is about four miles long, three-quarters of a mile wide and roughly rectangular in outline (Fig. 1). It is fed by four rivers at the south, the Dyfrdwy, Twrch, Llafar and Glyn, and to the north is drained by the Dyfrdwy (Dee) which flows to the Irish Sea via Llangollen and Chester. The land surrounding the lake is agriculturally poor, largely hill and moorland, and is mainly used for sheep-grazing. The lake water is soft, slightly acid or neutral, and poor in electrolytes (Table 1). The electrical conductivity has been determined as 38–45 μ mho, placing the lake in the oligotrophic category of Danish workers (Dunn, 1952), and the character of the rooted vegetation, mainly *Litorella* sp. and *Isoetes* sp., conforms

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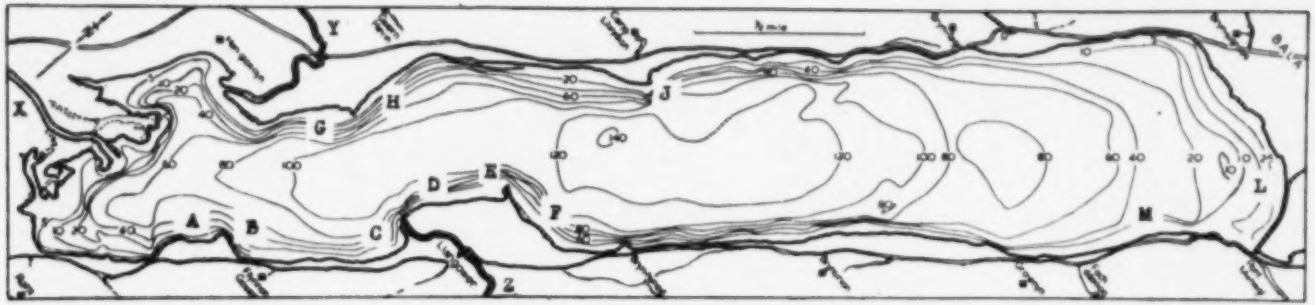

Fig. 1.—Llyn Tegid (Bala Lake), showing the regular netting stations A-H. Stations occasionally netted, J. L. M. The main tributary streams are X, Afon Lliw ; Y, Afon Llafar ; Z, Afon Glyn. The Rhydwen is about 1½ miles south-east of Station A (Nat. Grid. 23/912303). The Upper Afon Lliw is about 3 miles west of X (Nat. Grid. 23/832323).

to the early mesotrophic category of Pearsall (1921). Dunn (1952) has discussed the status of Llyn Tegid in relation to the general problems of classification of evolving lakes, concluding that Llyn Tegid is in the last stages of oligotrophy. The fish fauna of the lake conforms with this view, including the

TABLE 1

Chemical analysis of Llyn Tegid water by Dr E. Gorham of the Freshwater Biological Association. Samples taken in mid-lake in 1955, A at 5 metres depth, B at the bottom 25 metres depth.

		A	B
pH		5·87	6·32
SiO_2	p.p.m.	2·0 (mixed samples)	
Ca	,,	2·6	4·1
Mg	,,	0·5	0·6
Na	,,	3·7	3·7
K	,,	0·6	0·6
Cl	,,	6·3	6·3
SO_4	,,	4·9	4·9
HCO_3	,,	4·2	8·8
Total ions	m/equiv/litre	0·348	0·424

species characteristic of oligotrophic lakes (trout, grayling, gwyniad) together with some typical of eutrophic waters (perch, roach, pike).

Fig. 1 shows the contours of the lake in feet, according to the survey made in 1951. In most places the shore falls steeply to about 60 feet (20 metres) and then more gradually to a maximum depth of 140 feet (about 47 metres). Thus the greater part of the lake is over 20 metres deep. When the thermocline forms in summer, the hypolimnion is large in comparison with the total volume of the lake, and Dunn (1952) has shown that there is little diminution in the oxygen content of the deeper waters at this time.

In dividing the lake bottom into faunal zones, Dunn (op. cit.) has proposed three divisions : the *littoral*, from the shoreline to the lower limit of rooted vegetation at about 3 metres, the *sublittoral* from 3 metres to the depth at which a truly profundal fauna is obvious, at approximately 15 metres, and the *profundal*. She showed that the littoral fauna is richest in species, the sublittoral poor in both species and numbers, and that the profundal fauna consists

TABLE 2

The number of trout caught each month in the lake.

	1952	1953	1954
January	—	64	32
February	—	13	74
March	—	80	62
April	—	133	176
May	—	143	253
June	—	130	97
July	—	8	12
August	—	10	27
September	—	27	19
October	—	48	10
November	—	—	5
December	41	100	—
			Total 1,564

TABLE 3

The monthly distribution of the stream samples and the number of trout in each sample.

River	Month	Number of trout
Afon Lliw	Oct. 1953	125
	Feb. 1954	43
	March 1954	28
	May 1954	11
	Aug. 1954	12
Afon Glyn	June 1953	64
	Sept. 1953	22
	May 1954	84
	Aug. 1954	42
	Nov. 1954	36
Upper Afon Lliw	Oct. 1953	42
	Dec. 1953	41
Rhydwen	Sept. 1955	917

of only seven species, of which the number of individuals " frequently equalled or exceeded that of the total littoral species ".

The trout is one of the most abundant fish in the lake, and large numbers of roach, perch and gwyniad are also present. The grayling, which, like the trout, lives mainly in the littoral waters, is comparatively scarce : between October and March, 1953–54, seine nettings caught 130 trout but only 17 grayling. The opportunity for a survey of the biology of the trout arose in 1952 when the Welsh Land Sub-Commission, which controls the lake and surrounding estate gave permission for these fish to be caught for scientific purposes. The present work is an account of some of the results of this survey.

2. METHODS AND TERMINOLOGY

From December 1953 to October 1954 the lake was netted intensively at all seasons, using a conventional cotton drag net, often called a shore seine, or simply a seine. The lake was usually netted at least once each week, but this was not always possible and few trout were caught in some months (e.g. February 1953, November 1953 and 1954). Data from all the fish caught in each calendar month were combined and treated as if obtained from a single large sample taken in the middle of each month. The numbers of fish caught each month are given in Table 2.

The net had a mesh of $\frac{1}{4}$ inch knot to knot, and was 90 feet long and 12 feet deep. It was mounted to hang vertically in the water with its cork line at the surface. In use, the net was laid parallel to the shore, about 60 feet out, and hauled on shore by means of ropes attached at the ends. Thus, only trout living in the littoral zone of the lake were caught, and those in the upper 12 feet of the deeper water, a fact which must be remembered when considering the results. The mesh retained trout longer than about 40 mm., a length exceeded during the first summer of life; the smallest fish caught in the net were about 80 mm. long and since the net could catch smaller fish it can be concluded that these 80 mm. fish were in fact the smallest fish in the lake, and that the mesh was not selective for size.

The shore in most places is steep and littered with large boulders, quite

unsuitable for seine netting, which was therefore confined to a few stations on the shore (Fig. 1). The regular stations A to H were generally visited each month, but strong onshore winds sometimes made netting ineffective or impossible at one or more of the stations. The number of draughts taken at each station and the catch of trout in each draught were recorded.

Trout were also caught in two of the tributary streams, the Glyn and Lliw, and in a moorland stream about four miles from the lake, the Upper Afon Lliw (Fig. 1), at the times given in Table 3. River trout were caught by means of an electric fishing machine, which stunned fish within a radius of 2 to 6 feet of a portable electrode. Except in the most turbulent water it was possible to capture all the trout which were stunned, by scooping them with hand-nets into buckets containing clean water in which they quickly recovered.

Most of the trout caught in the lake and rivers were killed on the spot and examined within an hour or two. Each was measured to the nearest millimetre from tip of snout to the tail-fork (using a measuring board) and weighed to the nearest gramme on a " Butchart " 200 gm. balance. Heavier fish were weighed on a 500 g. spring balance. The body cavity was opened by a ventral slit from the anus to the pectoral girdle, and sex and gonad condition noted. The stomach was removed from some fish and preserved in 10 per cent formalin for future examination of contents. For each fish, the place of capture, length, weight, sex, gonad condition and other data, were recorded.

Other trout were tagged and released as soon as possible after capture, using numbered squares of plastic (5mm. × 5mm.) mounted in the middle of a length of silver wire. The tag was secured in the dorsal musculature through a hole made by a red-hot needle and afterwards treated with 1 per cent mercurochrome. The tagged fish usually rested on the bottom for a few minutes, then swam away actively with no apparent damage to its swimming movements.

Each month, unless weather conditions made it impossible, a thermistor was used to take the temperature of the mid-lake water at metre intervals from surface to bottom. The temperature was also recorded in the streams when they were fished, and in the lake littoral waters at intervals.

In the field, scales were taken from each fish by scraping the body surface with a blunt scalpel. The number of rings on the scales of salmonids varies in different regions of the body (Esdaile, 1912 ; Bhatia, 1931), so the scales were always taken from a small area on the left side just in front of the dorsal fin and above the lateral line, the " shoulder " of the fish. This ensured that counts of scale rings for different fishes should be comparable. In the laboratory, scales were prepared for examination by immersion for at least twenty-four hours in a saturated solution of sodium borate which loosened the mucus and tissue debris. For examination, about ten scales from each fish were mounted in glycerine jelly on a glass slide. The rest of the scales were kept for future reference. Scales were examined by means of a vertical projector, at magnifications of approximately 50 and 170 times. All the scales were read for age on the assumption that the number of completed bands of winter rings equalled the age of the fish in completed years. Proof of the validity of this assumption is given later in this paper. By this means, the age of all the fish was determined. The type of ring, summer or winter, at the scale edge was

noted, and on most scales the number of rings in each seasonal band was counted. Counts were made on several scales from each fish and in nearly every case all the scales gave the same count. When this was not so, the variation in count was small, usually one or two, and the highest value was recorded.

The methods used in the examination of the stomach contents are given in a later paper (Ball, 1960).

Terminology

Year of life

The year of life is reckoned from the time of hatching. In §4 reasons are given for taking March as the month in which most Llyn Tegid trout hatch. Hence, each year of life starts in March.

Year class

The trout have a well-defined annual spawning season in autumn (Ball, 1957) producing eggs which hatch the following March. All fish spawned in one spawning season form a year-class, designated by the year of hatching. Thus, the 1952 year-class consists of fish which hatched about March 1952 from eggs laid the previous autumn.

Age group

An age group is a group of fish of the same age, and is designated by the age in Roman numerals with a plus sign. Thus the II + age group includes all trout in their third year of life (e.g. the 1951 year class in March 1953–February 1954). Trout move into the next age group on their " birthday ", 1st March. It is sometimes convenient to use the term ' age group ' to include fish of the same age but of different year classes in different years. For example fish of the 1951 year-class in June 1953, and fish of the 1952 year-class in June 1954 would be the same age, and could be collectively referred to as the II + age group. During their first year of life, trout belong to the O + age group.

Trout in II + age groups (i.e. in their third year of life) are termed two-year-old fish (or trout), or II + fish (or trout). Similarly we get three-year-old or III + trout, one-year-old or I + trout. The age of trout on or around 1st March can be referred to as age I, age II, age III and so on.

Length

The length of trout given in this work is the fork length i.e. the shortest measurement along the stretched body from the tip of the snout to the angle (tip of the shortest caudal fin-ray) of the forked caudal fin.

Maturity

Trout are said to be maturing or ripening when their gonads show definite signs (microscopic and/or macroscopic, according to the context) that they will produce mature sperm or ova at the next spawning season. Maturing gonads can be recognised macroscopically from July onwards. Females in advanced stages of maturity can generally be recognised without dissection, as the greatly enlarged ovaries distend the ventral region. Fish are said to be mature or running ripe when the sexual elements can be expressed by gentle

pressure on the ventral flanks. This can be done more easily in the male than in the female.

Spent fish

After spawning, when no more sperm or ova will be shed, the trout are said to be *spent*. There are no reliable external signs of spending. Unlike adult salmon, the smaller maturing trout encountered in this survey do not undergo a long fast, and are not noticeably emaciated when spent. Spent gonads are easily recognisable soon after spawning, but recognition becomes progressively more difficult with time, and four or five months after spawning macroscopic recognition of spent gonads is uncertain.

Alevin

The term alevin is used for the newly-hatched trout before the yolk-sac is absorbed.

Redd

The female trout makes a depression or bed in gravel in which she lays her eggs. She then covers up the eggs with displaced gravel (Jones & Ball, 1954). Such gravel in which eggs have been laid is termed a redd.

Migrant groups

Lake trout hatch in tributary streams and then migrate to the lake. They migrate during winter and spring, some in September–March, the majority in April–May (Ball & Jones, 1960). The period September–May can be referred to as the migration season. Each trout can be placed in a migrant group according to the age at which it migrated. For example all trout which migrated during the winter or spring in which they completed their second year of life are 2-migrants and constitute the 2-migrant group. Similarly there are 1-migrants, and 3-migrants.

Not all trout leave the tributary streams for the lake. Those which stay behind, whether permanently or only until the next migration season, are termed *resident stream trout*, or stream residents, in contrast to the *migrant trout*. Similarly in the lake during a migration season, the newly arrived *migrant trout* are distinguished from the *resident lake fish* which migrated in a previous season.

Note. In all graphs, unless otherwise stated, numbers by a point indicate the number of trout on which that point is based. A year-date (1950, 1951, etc.) by a curve indicates the year class to which the curve refers.

3. GROWTH OF THE SCALES

A. *Scale morphology*

Neave (1936, 1939) has given detailed accounts of the histology of the teleost scale. For present purposes, only the surface appearance of the scale is important, and is illustrated in Pl. 1A. The scale is an oval plate consisting of two layers, an inner layer of fibrous lamellae and an outer bony layer. *In situ* the anterior part of the scale is buried in a dermal scale pocket. Only the

posterior portion projects from the pocket and is visible externally through the transparent epidermis. The buried anterior part bears growth ridges, which appear as rings on the surface of the bony outer layer, some of which project a little way on to the posterior surface. These rings are formed successively as the scale grows in area ; according to Neave (1939) they are not produced by the secretory activity of special cells, as was formerly believed, but result from the presence of excess bone-forming material in the fluid between rows of scale-forming cells at the growing margin. These same cells are responsible for the production of the entire outer (bony) layer of the scale. When the scale is first laid down, growth in area is rapid and no excess material is available for ring formation ; hence the centre of the scale is a flat oval area without rings on its surface, termed the *scale focus* or *scale nucleus*. Outside this, resulting from slower growth in area, growth rings appear (Neave, 1939). The growth rings can be classified into two main types :

(a) Widely spaced rings, generally called wide rings, summer rings, or open-growth rings. Scales with wide rings at the edge are termed *open-margin scales*, or *wide-margin scales*.

(b) Closely-spaced rings, generally called narrow rings, winter rings, or closed-growth rings. Scales with narrow rings at the edge are termed *closed-margin scales*, or *narrow margin scales*.

Since the present work has shown that these two kinds of rings are formed summer and early winter respectively, they will be called *summer*, or *wide rings*, and *winter* or *narrow rings*, using the terminology applied to salmon parr scales by Jones (1949). As the scale grows, zones of many wide rings alternate with zones of a few narrow rings ; these zones are termed the *summer band* and *winter band* respectively, and the *seasonal bands* in joint reference.

Summer rings can be divided into two types (Jones, 1949) :—

(a) Wide summer rings, appearing at the beginning of the summer band, and

(b) Narrow summer rings, appearing outside these.

The distinction between the two types of rings is shown in Pl. 1B. It is not a sharp distinction : wide summer rings narrow gradually into the narrow summer type, which in turn narrow into winter rings. Narrow summer rings are not always distinguishable in the first summer band, but are nearly always recognisable in subsequent summer bands.

Winter rings

Four criteria serve to define winter rings : (i) they are much closer together than any summer rings, (ii) they look less robust than summer rings, (iii) they are generally irregular and broken, (iv) they rarely extend far round the antero-lateral shoulders of the scale (x–x in Pl. 1A). These characters are shown in Pl. 1 A and B. Plate 1 C shows how the winter rings usually do not extend as far round the scale margin as summer rings ; as a result of this, the first ring of a summer band usually embraces or *cuts over* the outer ends of the incomplete rings of the previous winter band (Pl. 1 B,). This cutting-over is unmistakable, and allows quick and certain identification of the complete winter band. In this connection, its value on coregonid scales has been emphasized by van Oosten (1923, 1929) and van Oosten & Hile (1949), and in

coarse fishes by Beckman (1943). Went (in Frost & Went, 1940) illustrates this cutting over on the scales of young salmon, and refers to it as a pseudo-spawning mark.

True spawning marks, scars on the scale surface interrupting the normal succession of rings and resulting from scale absorption during the spawning period, have not been identified with certainty in Llyn Tegid trout.

Summer checks

On some scales, a few narrowly-spaced rings occur in the middle of a second or subsequent summer band. This is a summer check (Pl. 1D, at S). Summer checks are distinguishable from true winter bands by the fact that their constituent rings are usually regular and unbroken, and extend round the lateral areas of the scale ; by the absence of preceding narrow summer rings ; and by their position between two bands of wide rings, each band being much narrower than a typical summer band at the same age.

Summer checks have been observed by most workers on fish scales and Jones (1949) has described and illustrated them on the scales of young salmon.

Accident scales

Especially in the case of older trout, it was often found that some, occasionally all, of the scales mounted for examination had a very large central area, unsculptured and much bigger than an ordinary scale nucleus, outside which normal rings appeared (Pl.1D). These *accident scales* were never used in age determination ; when necessary, more scales from the same fish were examined until a normal scale was found. Neave (1939) has described the formation of accident scales, which are produced following the loss of the original scale from its pocket. A new scale is quickly formed in the old pocket ; its growth is at first so rapid that all available bone-forming material is used for growth in area and no rings are formed. Only when growth of the new (accident) scale slows down as it approaches the limits of the scale pocket is surplus material available for ring formation.

Accident scales occur much more frequently on trout in moorland streams than on trout caught in the lake, perhaps because, especially in flood conditions, stream trout are more likely to lose scales in being buffeted against rocks and other obstacles on the stream bed.

Curious accident scales with multiple centres are formed when the original scale is not lost but only partially dislodged and moved in its pocket. Following dislodgment, the scale grows about a new centre instead of about the original scale nucleus (Pl. 2A and B).

B. *The scales of Llyn Tegid trout*

Scales were available for every month from December 1952 to October 1954, excepting November 1953. Very few fish less than one-year-old or more than five-years-old were caught, so that the conclusions strictly apply only to trout in their second, third, fourth and fifth years.

Throughout this section "growth" is to be understood as referring to *scale growth* unless otherwise stated.

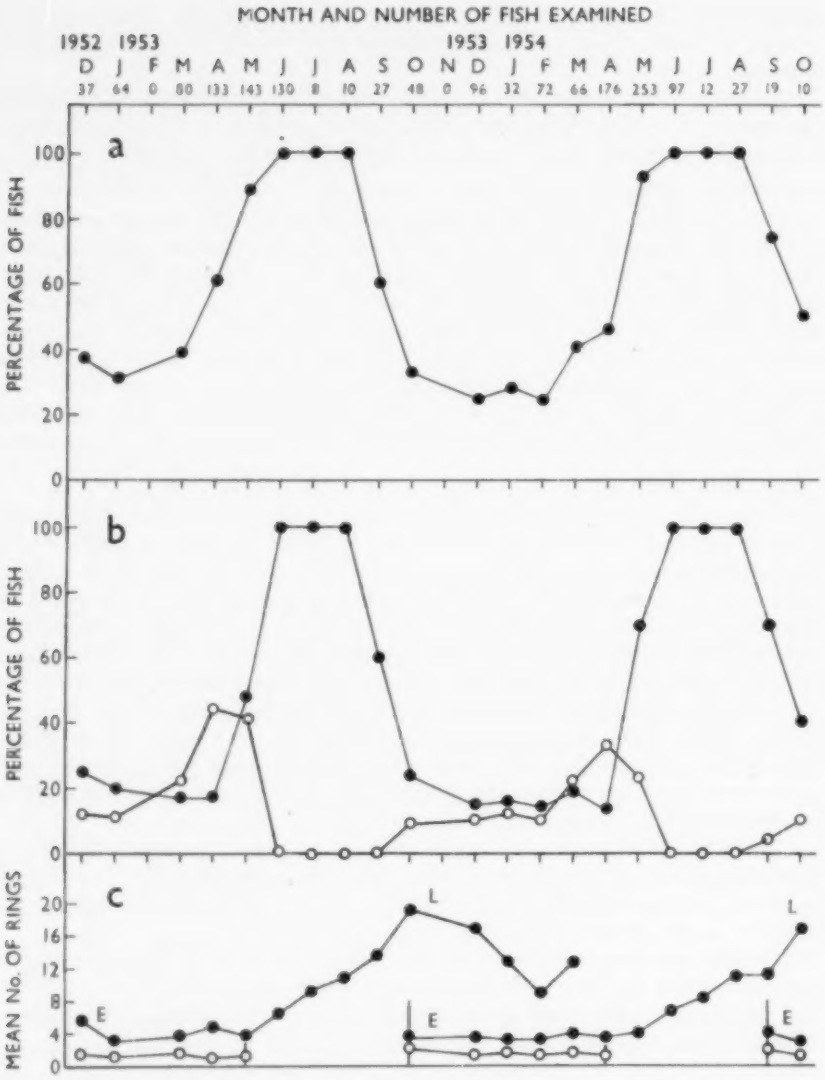
MONTH AND NUMBER OF FISH EXAMINED
1952 1953 1953 1954
D J F M A M J J A S O N D J F M A M J J A S O
37 64 0 80 133 143 130 8 10 27 48 0 96 32 72 66 176 253 97 12 27 19 10
a
b
c
PERCENTAGE OF FISH
PERCENTAGE OF FISH
MEAN No. OF RINGS
0 20 40 60 80 100
0 4 8 12 16 20
E
L
E
L
E

Fig. 2.—(a) Percentage of fish with wide margin scales. (b) Percentage of fish with 1 or 2 wide marginal rings o——o. Percentage of fish with 3 or more wide marginal rings ●——●. (c) Mean number of wide marginal rings 1 or 2 o——o, 3 or more ●——●. E—early growers. L—late growers.

I. *The seasonal occurrence of growth rings*

Fig 2 a shows the monthly percentage of fish with open-margin scales (i.e. with wide rings at the scale margin). Clearly in a general sense the alter-

nation of slow and rapid scale growth is a seasonal effect. Wide rings are typical of summer (April–May to September–October), narrow rings of winter (September–October to April–May), and the bands of rings are correctly termed summer and winter bands in Llyn Tegid trout.

The occurrence during the winter months of fish with open margin scales needed further investigation. To accomplish this, it was decided to distinguish between fish which had recently started rapid scale growth and fish well advanced in a period of rapid growth. This was done for each monthly sample by dividing the fish with open margin scales into two groups :

(i) Fish with one or two wide rings at the scale edge (recently started in rapid growth).

(ii) Fish with three or more wide rings at the scale edge (well advanced in rapid growth).

The monthly mean number of marginal rings was determined for each group. Results are presented graphically in Figs. 2 b and 2 c. The summer and winter periods will be considered separately.

II. *The growth of scales during the winter* (October–March)

Three types of scales were found to occur during winter :

Type A : Open margin scales with only a few (1–5) wide rings outside the last winter band. These formed 20 to 30 per cent of the winter samples.

Type B : Open margin scales with many marginal wide rings (10 or more). These formed less than 10 per cent of the winter samples.

Type C : Closed margin scales with a few (less than five) marginal narrow rings. These formed about 70 per cent of the winter samples.

The results for the winter of 1953–54 will be considered in detail. Results for December, January and March of the previous winter were similar (Table 4).

TABLE 4

Scale analysis results for the winter of 1952–53. Percentage representation in the samples of fish with the different types of scales. The figures in brackets give the mean number of rings in the marginal band.

Month	No. of Fish	Type A scales		Type B scales	Type C scales
		1 or 2 wide marginal rings	3 or more wide marginal rings		
Dec. 1952	41	12% (1·5)	10% (2·2)	15% (12·5)	63% (2·0)
Jan. 1953	64	11% (1·5)	10% (2·2)	10% (11·1)	69% (1·9)
March 1953	78	22% (1·5)	16% (2·4)	2% (9·5)	60% (2·0)

Type A scales

Relevant data are given in Table 5.

Fish with *Type A* scales first appeared in October, and occurred in the same relative numbers in the samples from October to February. In this period the mean number of marginal wide rings also remained constant (Table 5) the monthly means having been shown by the *t* test (Simpson & Roe, 1939, pp. 209–210) to be not significantly different from assumed means of 3.0 and

TABLE 5

Scale analysis results for the winter of 1953–54. Percentage representation in the samples of fish with the different types of scales. The figures in brackets give the mean number of rings in the marginal band.

Month	No. of Fish	Type A scales		Type B scales	Type C scales
		1 or 2 wide marginal rings	3 or more wide marginal rings		
Sept. 1953	27	0	0	60% (13·6)	40% (2·4)
Oct. 1953	48	9% (2·0)	15% (3·3)	9% (19·2)	67% (2·5)
Nov. 1953	0	—	—	—	—
Dec. 1953	100	10% (1·2)	10% (3·4)	5% (16·8)	75% (2·6)
Jan. 1954	32	12% (1·6)	16% (2·8)	0	72% (2·3)
Feb. 1954	74	9% (1·0)	7% (2·8)	9% (8·8)	75% (2·5)
March 1954	62	20% (1·6)	10% (4·0)	10% (12·8)	60% (2·3)

1.75. It follows that during the period October–February, these fish did not add to their scale margins. They must have formed the current winter band in August-September, when they would be included in the 40 per cent September fish with closed margins, commenced rapid growth for a short while, then ceased all growth in October until the following March or April, when new wide rings were formed outside those produced in September and October. The March increase in the percentage of *Type A* fish with one or two marginal wide rings was probably caused by some of the *Type C* fish resuming rapid growth (see below) and so coming in the *Type A* category.

The rest of the *Type A* fish, those with three or more wide marginal rings, stayed fairly constant in numbers from February to March, but the mean number of marginal wide rings on their scales increased significantly ($t=2·7$, $P=0·04–0·05$), indicating the resumption of rapid growth. In effect, *Type A* fish started their summer growth the previous autumn : they will therefore be called *early growers*.

Type B scales

By analogy with the early growers, it seems most probable that *Type B* scales are from fish which stopped rapid growth in October without forming the current winter band, so that when caught during the winter they appeared to be continuing a long bout of rapid growth. They will be called *late growers*, using the term simply to describe the appearance of the scales. The mean number of wide wings in the outermost band of these scales reached a maximum of 19 in October (Fig. 2 c), but so few late growers were caught (one to six each month) that results obtained from them must be treated with caution. Three late growers were found in April, 1954, but none after this ; whether this was because all had formed a winter band in April–May or because, though present after April, they escaped capture, cannot be decided. The formation of a winter band in April–May does not seem likely, since results from examination of scales (see below § BIII) and from monthly mean lengths for age (§ 4 A) indicate that this is a time when most trout grow rapidly.

If the late growers continued rapid growth in April–May they would

subsequently give anomalous scale readings and show " summer " bands containing abnormally high numbers of rings. Such fish would occur only occasionally in the samples, and might not always be recognised and their scales interpreted correctly, but being numerically insignificant they should not seriously affect results obtained from large samples. Five fish have been found with scales showing an extremely wide summer band and which appeared from scale readings to be a year younger than their size suggested. These fish may well have been late growers during an earlier winter when they did not form a winter band.

Type C scales

Fish with closed margin scales were predominant in the winter samples. Since the appearance of the scales suggested that the fish were growing slowly at the time of capture, they will be termed *slow growers*. The mean number of marginal narrow rings on such scales was constant from September to March (Table 5). The percentage of fish in this condition was certainly constant from December to February. The slight rise in the percentage of slow growers from October to December, if significant, must have been the result of some late growers forming the winter band and so entering the ' slow growing ' category. These results lead to the conclusion that the scales of slow growers did not grow from October to February.

Supporting evidence for this interpretation is provided by the scales of a trout tagged in May 1954 and recaptured successively on 9. x. 53, 21. x. 53, 5. i. 54 and 9. iii. 54. At each recapture the fish was measured and returned to the lake after the removal of a few scales from within a small area on the shoulder. Typical scales taken on these occasions are shown in Pl. 3. Clearly there was no addition to the marginal narrow rings from October 1953 to April 1954. This fish grew normally during the summer, so it is very unlikely that the absence of growth in the winter is an abnormal effect due to tagging. No other trout were recaptured at such times as their scale structure could either support or refute the idea that scale growth ceases for a while in winter. All the fifteen fish tagged one summer and recaptured the next, did, however, show the formation of one winter band on their scales, thus confirming the annual nature of the winter band.

Allen (1938) gives some results from his tagged fish. From November to February, he records three fish as showing no scale growth, one as having added one narrow ring, and one as adding two wide rings. This last fish was probably a late grower. The data given by Allen from recaptures made over longer periods indicate that narrow rings are formed annually at some time in the winter. Allen (*op. cit.*) suggests an ' overlap ' theory to account for the appearance of wide marginal rings on scales taken during the winter, involving the production of narrow rings at different times during the winter by different individuals : at any time in the winter, some fish will then be forming narrow rings, others wide rings. However, the present results (Table 5) favour the interpretation adopted here, that narrow rings are formed by most fish at the beginning of winter, and that for a period (November–February) there is no growth of the scales. Such results based on samples taken through the winter

period, probably furnish a more reliable indication of what really happens than the examination of different scales from a few fish taken at different times, in view of the variations in ring counts made on scales from different parts of the body of salmonids (Esdaile, 1913 ; Bhatia, 1931).

Some of the slow growers started rapid growth again in February–March : a fall of 15 per cent in the slow growers (Table 5) was accompanied by a rise of 11 per cent in the early growers with one or two marginal rings. The percentage of open margin scales then increased each month to 100 per cent in June (Fig. 2 b).

Other data

For the winter 1952–53, only the December, January and March results were of any significance, since only thirteen fish were caught in February.

Results of scale analyses of fish caught in the winter 1952–53 are given in Table 4. It will be seen by comparison with Fig. 2 and Table 5 that these results are substantially the same as those presented in detail for winter 1953–54, the main difference being the greater number of late growers taken in 1952–53.

An important conclusion emerging from the results on winter scale growth is that the winter band is an annual structure. This confirms that the age of Llyn Tegid trout can be assessed in the usual way, by counting the number of completed winter bands.

III. *The growth of scales during the summer (April–September)*

The start of summer growth was indicated in 1953 and 1954 by a rise in the percentage of fish with one or two open rings at the scale edge, from February to April (Fig. 2 b). This was followed by an increase in the percentage of fish with three or more marginal open rings, which reached 100 per cent in June.

Table 6 shows the monthly representation of fish in each year class with open margin scales in spring 1954. These results show that younger fish tend

TABLE 6

Percentage number of fish with open margin scales in each year class in the spring of 1954. Excluding late growers. Size of sample in brackets.

Month	Year Class			
	1953	1952	1951	1950
Feb. 1954	—	30 (23)	27 (22)	7 (13)
March 1954	—	66 (3)	37 (20)	24 (25)
April 1954	—	46 (92)	37 (54)	22 (18)
May 1954	100 (20)	94 (174)	84 (37)	57 (7)
June 1954	100 (8)	100 (73)	100 (13)	100 (3)

to start rapid growth earlier in the spring than older fish. This phenomenon has previously been reported in *Salmo* (Southern, 1935 ; Went & Frost, 1942 ; Nümann & Sella, 1943), *Salvelinus* (Cooper, 1951), and *Coregonus* (Nümann & Sella, *op. cit.*).

Throughout the summer, the continued rapid growth of scales is indicated by the increase in the mean number of marginal wide rings at a rate of two or three per month (Fig. 2 c). For most fish in 1953, the rapid growth season

ended in September–October, but a few late growers possibly continued rapid growth into the winter period. For the rest, the rapid growth season extended from March or April to September or October. The 1954 growth season was rather longer than the 1953 season : in October 1954, 33 per cent of the fish were continuing the summer growth, whereas only 9 per cent were in this state in October 1953.

Narrow summer rings

In July and August of both years, some fish were forming narrow summer rings, and this type of ring was present on all open-margin scales in September. This phenomenon, which has been fully described in salmon parr by Jones (1949), who also found it in Llyn Tegid trout (Jones, 1953), and which is suggested by the results of Frost (1950) for brown trout in Caithness, indicates that scale growth in the second half of summer (July–September) was slower than in the first half (April–June) ; the narrow summer rings were nearer together than the ordinary summer rings and were formed at the same rate (Fig. 2 c).

IV. *Variations in ring-count with age*

It was noticed during examination of scales that the number of rings in the summer bands on individual scales decreased progressively from the first or

TABLE 7

The mean number of rings in the 1953 summer band on scales of fish of different ages caught in the lake during the winter 1953–54. Number of fish in brackets.

		Month of Capture		
Year-Class	Age Group	Oct. 1953	Dec. 1953	Jan. 1954
1952	I+	15·6 (15)	14·1 (21)	12·9 (8)
1951	II+	17·0 (18)	14·6 (24)	14·9 (14)
1950	III+	12·7 (9)	12·0 (7)	13·7 (6)
1949	IV+	8·0 (1)	8·0 (1)	9·0 (3)

second summer band outwards. Table 7 gives the mean number of rings formed on the scales of fish of different ages in summer 1953. Counts of scale rings for stream fish in the same summer are given in Table 8. Both tables

TABLE 8

The mean number of rings in the 1953 summer band on the scales of fish caught in Afon Lliw in October 1953. Number of fish in brackets.

Year Class	Age Group	Number of rings
1952	I+	15·3 (56)
1951	II+	9·6 (20)
1950	III+	6·5 (8)
1949	IV+	—
1948	V+	3·7 (3)

show that, over a given period, among fish living in the same environment, the number of summer scale rings formed varies inversely with age, a phenomenon previously described by Masterman (1913) in adult salmon caught in fresh water. The fact that in Table 7 I + fish gave a lower count than II + fish is probably due to the migration of fish from the stream into the lake

(Ball & Jones, 1960). Briefly, most of the I + fish included in Table 7 spent the summer of 1953 in tributary streams, migrating to the lake in late summer and autumn. Since the rate of growth, and the number of summer rings formed is less in the streams than in the lake (see § 4 and Tables 7 and 8), the count for I + fish given in Table 7 is not truly comparable with the counts for older fish, nearly all of which spent the summer in the lake. Consideration of Table 8 suggests that had the I + fish included in Table 7 also spent the summer in the lake, they would have given a higher summer ring count than the II + fish.

4. GROWTH OF THE BODY

Previous studies of the growth of trout in the British Isles have been based on lengths back-calculated from scales e.g. Allen, 1938, Swynnerton & Worthington, 1939 ; Went & Frost, 1942 ; Frost, 1950 ; Frost & Smyly, 1952 ; Frost, 1956 ; Swan, 1957. In the present work, lengths of fish of known age were available for most months from December 1952 to October 1954, and back-calculated lengths were therefore not used to study growth. It was shown above that the correct age of trout can be determined by counting the winter bands on the scales, so that trout growth has been studied by comparing the mean sizes of trout of different ages.

A. *Seasonal growth of Lake trout*

I. *Growth in length*

Seasonal growth curves for each year class sampled in sufficient numbers are given in Fig. 3. In Fig. 3a the curves are drawn through the mean lengths of each year class in the monthly samples and are markedly irregular especially during the winter months. The smoother curves of Fig. 3b were obtained by grouping the monthly samples in pairs to produce bi-monthly mean lengths.

The growth curves show clearly that the growth rate varies seasonally with rapid growth from March–April to September–October. The same effect appears in the monthly length-frequency histograms for the 1952, 1951 and 1950 year classes in Fig. 4. There is a period from about October to March in which little or no growth occurs, corresponding to the period in which the scales do not grow. The growth curves show pronounced irregularities at this time, probably due to the rather small numerical size of the winter samples. There are also two biological factors which will contribute to these irregularities:

(i) From September to April, one-two- and three-year-old trout migrate from tributary streams to the lake, most of them entering the lake in April (Ball & Jones, 1960). Growth in the lake being faster than in the tributary streams (§ 4 C), resident two- and three-year-old trout in the lake will be longer than their contemporaries in the streams. It follows that the entry of 2- and 3-migrants will depress the mean lengths of their year classes in the lake, and will tend to produce irregular and widely dispersed length-frequency distributions, as in Fig. 4. This effect is most marked, as would be expected, at the time of the big spring migration to the lake in March–April (Fig. 3).

(ii) The mean length of the 1950 year class tended to fall throughout the winter 1953–54. At this time, these trout were nearly four-years old, and were

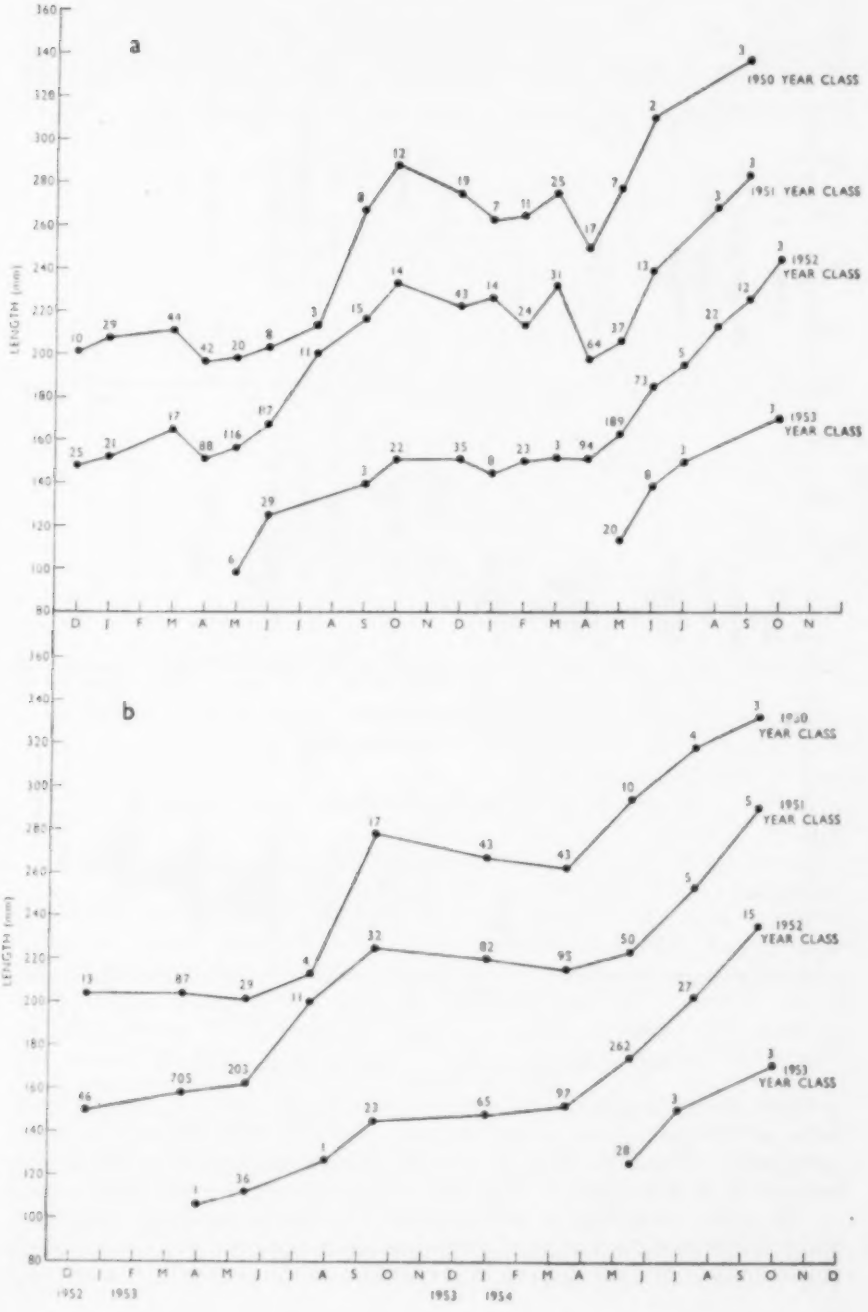
a
1950 YEAR CLASS
1951 YEAR CLASS
1952 YEAR CLASS
1953 YEAR CLASS
LENGTH (mm)
D J F M A M J J A S O N D J F M A M J J A S O N
b
1950 YEAR CLASS
1951 YEAR CLASS
1952 YEAR CLASS
1953 YEAR CLASS
LENGTH (mm)
D J F M A M J J A S O N D J F M A M J J A S O N D
1952 1953 1953 1954

Fig. 3.—Seasonal growth curves for lake trout. (a) Based on monthly mean lengths. (b) Based on bi-monthly mean lengths.

all 2- or 3-migrants, having been living in the lake for one or two years. Obviously, the decline in mean length of this year class cannot be an effect of migration from the streams. An explanation is suggested by the increasing density index of resident lake fish of all year classes during the winter, which

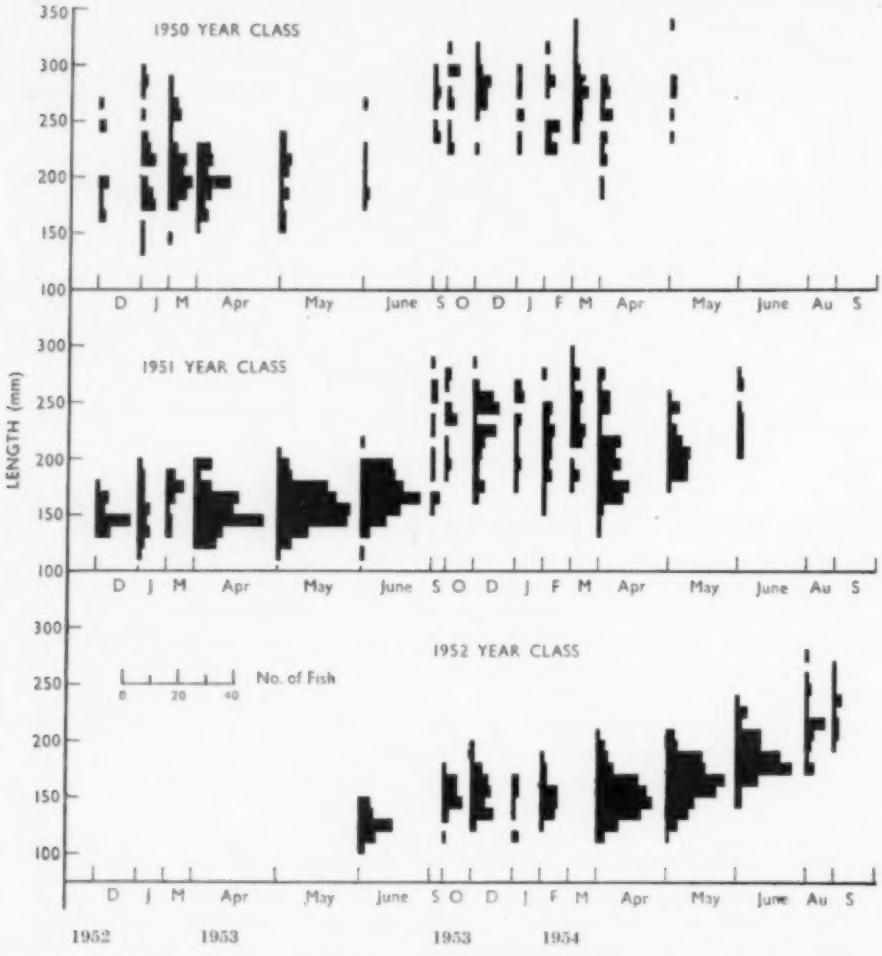

Fig. 4.—Length-frequency histograms for lake trout.

is interpreted as resulting from the progressive movement of resident trout from sub-littoral waters to the shallows (Ball & Jones, 1960). The most acceptable explanation of the fall in mean length accompanying this process is that larger fish tend to move to the shallows before smaller fish of the same age.

The effect of migration in depressing the mean length is eliminated in Fig. 5, which shows the growth curves for different migrant groups in 1953–54. These curves display the same pattern of seasonal growth as those of Fig. 3 showing

that migration does not in any essential way distort the picture of seasonal growth inferred from Fig. 3 and the length-frequency histograms. Here also the mean lengths of the older resident lake fish (i.e. the two top curves, the 2-migrants of the 1951 year class, and the 1950 year class) tends to decline during the winter, probably because of the later return of the smaller fish from the deeper waters.

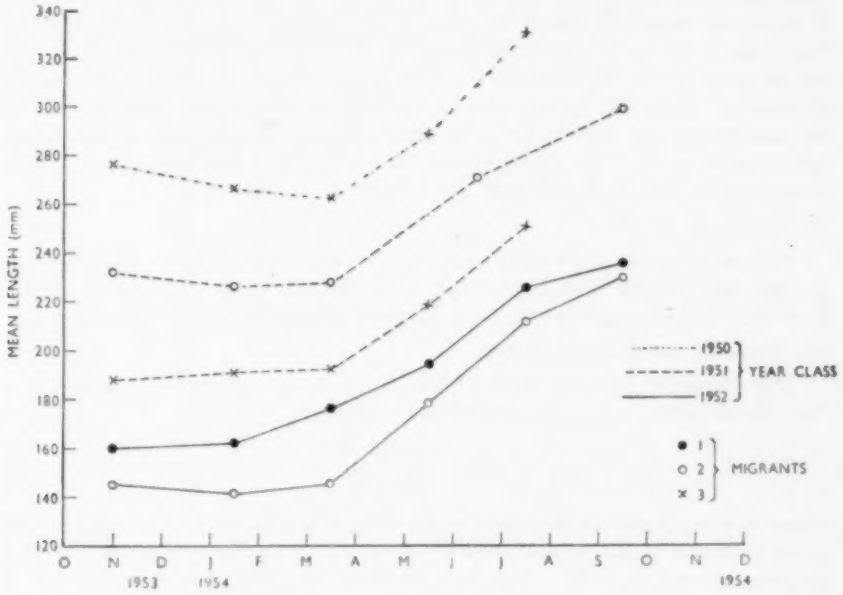

Fig. 5.—Growth curves for different migrant groups in the lake.

Slight growth from February to March is indicated by the length frequency histograms for the 1950 and 1951 year classes in 1954, and seems to be followed by a loss of the largest fish between March and April. It has been found that older fish precede younger individuals in the spring migration away from the littoral (Ball & Jones, 1960), and this change in length frequency histograms suggests that within a year class the larger individuals leave first. Rapid growth is shown by all the year classes from April onwards (Figs. 3 and 4). The end of the period of rapid growth, from the growth curves and length-frequency histograms, is in September or October.

Rate of growth during summer

During the summer (May–September) there is no migration from the tributary streams or from deep to shallow water (Ball & Jones, 1960). The growth from May to September shown by the curves in Fig. 3 may therefore be considered the real growth made by trout in the lake in this period, and specific growth rates calculated from the curves can be compared with the mean

specific growth rate of trout tagged and recaptured during the summer. Only the growth of the 1952 year class in the summer of 1954 will be considered, since most of the tagged fish belonged to this year class.

In April, May and June 1954, 119 fish of the 1952 year-class were tagged. Thirteen of these were recaptured in the same summer, the last recapture being on the 25th August. The mean specific growth-rate of these tagged fish was 0·305 per cent length per day (=2·135 per cent length per week). For fish of this year class, the mean lengths of the monthly samples from April to September 1954 lie on a straight line (Fig. 3) with a slope corresponding to a specific growth rate of 0·323 per cent length per day (=2·261 per cent length per week). Thus the specific growth rate indicated by the mean lengths of the samples is very close to the mean of the specific growth rates of individual fish, confirming that the slopes of the curves in Fig. 3 correspond to the true mean growth rate of trout during the summer.

II. *Growth in weight*

Curves for growth in weight have been constructed from the mean weights for age each month from September 1953 to September 1954 (Ball, 1957). Growth in weight parallels growth in length and calls for no special comment.

III. *Seasonal changes in condition*

The condition or well-being of fish is generally expressed in terms of a " ponderal index ", C in the generalised equation

$$C = \frac{\text{weight } 10^4}{\text{length}^n}$$

where n is an exponent determined by measuring the slope of a straight line fitted to a plot of log-weight against log-length, as in Fig. 6. From Fig. 6 in the present case n=2·92. This is sufficiently near n=3 to permit the use of the usual condition factor K, employing the cube of the length,

$$K = \frac{\text{weight } 10^4}{\text{length}^3}$$

which yields value for K of about 100 if the metric system is used. Allen (1938) similarly justified his use of K for trout in Windermere.

It is generally assumed that changes in the value of K reflect changes in the well-being of the fish. This assumption has often been questioned (e.g. Kesteven, 1947 ; Martin, 1949), and in the case of the herring, *Clupea pallasii*, Tester (1940) showed that there was no correlation between oil content, or fatness, and K. Obviously the value of K will change with large variations in the shape or density of the fish, which will affect the length-weight relationship and hence the value of n in the generalised equation for C ; for this reason, K does not provide a reliable method of comparing the condition of fish in different habitats or of different sizes, unless the length-weight relationship is first shown to be the same ($n \simeq 3$) in all the habitats and at all sizes.

In the present work, the length-weight relationship has been shown to be constant over the size range involved and in the different habitats (Fig. 6), so the use of K to measure condition is justified.

For lake fish, K has been calculated for every individual measured and weighed in the monthly samples of each year class, excluding ripening and recognisably spent fish. The seasonal cycle in the mean value of K which emerges is therefore independent of the annual cycle of sexual maturation. K for all the year classes shows the same pattern of seasonal change, so the

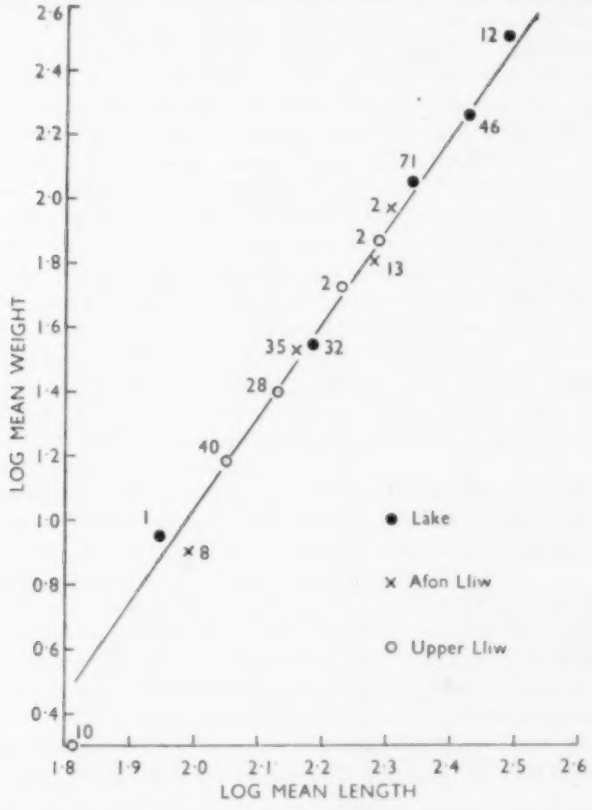

Fig. 6.—Length-weight relationship. Logarithmic plot of mean weight against mean length for trout from the lake, Afon Lliw and the Upper Afon Lliw.

values have been combined to give the mean K for all fish in Fig. 7. This diagram also shows the seasonal changes in the amount of fat present between the pyloric caeca and around the stomach. This is the main food store of trout (Swift, 1955), and was assessed by visual classification of the fat as ' poor ' (1 point), ' moderate ' (2 points), ' abundant ' (3 points) and ' very abundant ' (4 points). The total number of points gained by each monthly sample was divided by the number of fish examined to give an index of the mean amount of reserve fat, which is plotted in Fig. 7. Clearly, K is correlated with the amount of food reserve in brown trout, and hence with well-being or

condition, unlike the herring investigated by Tester (1940). Swift (1955) investigated seasonal biochemical changes in brown trout kept in a stew pond, using precise biochemical methods, and showed that fat in the gut wall was the principal store of food and that the amount of fat stored varied seasonally ; his results (fat reserves as percentage of the body weight) are shown at the top of Fig. 7. Swift's figures lag those for Llyn Tegid trout by

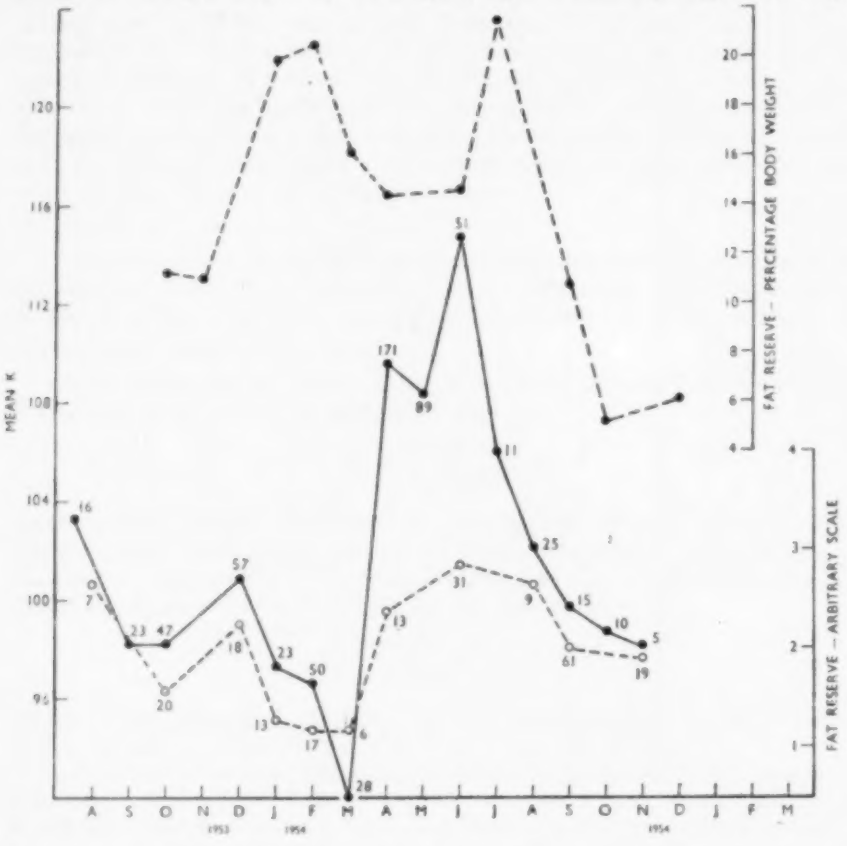

Fig. 7.—Seasonal changes in the mean condition factor K ●——●, and fat reserves according to the present work ○- - - ○ and Swift (1955) ● - - - - ●

about a month, which perhaps results from his fish being artificially fed to satiation or from local environmental differences, but the two curves are remarkably similar considering the widely different environments and methods. Swift suggested that the winter increase in fat reserves was due to his trout being artificially fed, but this effect is also shown by the wild Llyn Tegid fish and so must be a natural feature of trout biology. Qasim (1957) has shown that K for the shanny (*Blennius pholis*) has a seasonal cycle which is independent of the sexual cycle, and very like that of brown trout, with a major peak in

June and a minor peak in December-January. Like the trout, the shanny does not grow during the winter. Possibly the accumulation of reserve food during the winter period of arrested growth is a general phenomenon in temperate-zone fishes.

The close correspondence between the curves for K and for fat reserves during the winter (Fig. 7) suggests that the winter increase and decrease of K is entirely due to changes in food reserves. The present results, and those of Swift, indicate that the fat reserve in summer is not much greater than in winter, but K is much higher in June than in December. This raises the possibility that other factors in addition to the amount of stored food are involved in the increase in K from March to June. Growth begins at this time, and it is quite possible that at first individual growth in length is slower than growth in weight, resulting in high individual values of K. If this be so, then growth in length must catch up with growth in weight in mid-summer, when K declines from June to August although the fat reserves remain at a high level. However the scale used for assessing the fat reserves is arbitrary and coarse. This could be obscure differences in the summer and winter fat reserves, since the category ' very abundant ' includes fish with widely varying amounts of fat. Factors other than changes in food reserves might not be as important in producing the spring increase in K as Fig. 7 suggests.

Like K and the fat reserve, the food intake declines from a peak in about June to a lower summer level in the period July–October (Ball, 1960) ; this may cause a depletion of the food reserves in order to maintain growth, and hence the decline in the stored fat.

The extremely low values obtained by Swift for the fat reserves in the second winter are probably due to the fact that his fish became sexually mature in October (Swift, 1955). No data concerning the effect of sexual maturation on fat reserves were collected in the present work.

In the Atlantic salmon, the value of K rises rapidly in spring and early summer and declines in late summer and autumn in both parr and adult fish in freshwater (Hoar, 1939), thus resembling the changes in K of brown trout in spring and summer. Hoar also found that K increases with the age of the parr : in one river, K for one-year old parr was 100, for two-year-old parr 106, and for three-year old parr 116. In contrast K for Llyn Tegid trout declines slightly with age. At age II, K = 99·1, at age III, 96·2, age IV, 92·3 and age V, 91·6.

B. *Seasonal growth of stream trout*

No data are available concerning the seasonal pattern of growth in the moorland streams, since the Rhydwen and Upper Lliw samples were all taken during the autumn and winter. Samples were taken at different seasons in the tributary streams, which enabled seasonal growth curves to be constructed, though these are less detailed than those for the lake (Fig. 8).

I. *Growth in length*

Seasonal growth in the Glyn and Lliw follows the same pattern as in the lake. The Lliw curves indicate little or no growth from October to February, and the start of growth by most fish in February, about a month earlier than in the lake. This start of growth is also shown by the scales : in the March samples from the Lliw, the scales of sixteen out of twenty-five fish (64 per cent)

showed wide marginal rings compared with ten out of forty-two (24 per cent) in February. Growth then continues at least until August. The Glyn curves, though the samples are more widely spaced, appear to follow essentially the same pattern ; the discrepancy between the mean lengths of Glyn and Lliw trout in May is possibly due to the migration of larger fish to the lake in April

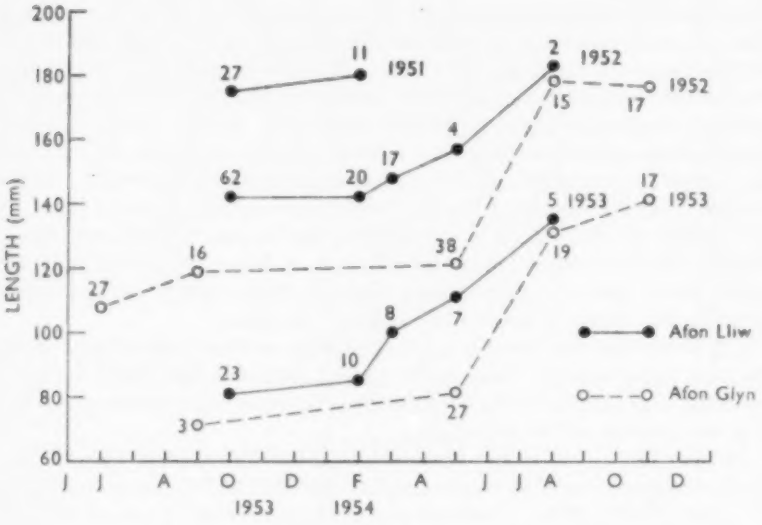

Fig. 8.—Seasonal growth curves for trout in Afon Lliw and Afon Glyn.

(Ball & Jones, 1960), but the data are clearly unsatisfactory in view of the small size of the Lliw samples and the wide spacing of the Glyn samples. The annual growth curves for the two streams (Fig. 10) are essentially similar, suggesting that the differences in growth rate indicated by Fig. 8 are due either to the inadequate samples or to slightly different patterns of seasonal growth in the two streams. Further work is needed to decide the issue.

II. *Growth in weight*

As in the case of lake trout, the weight curves are similar to those for length and call for no special comment (Ball, 1957).

C. *Annual growth of trout*

I. *Growth in length*

The annual growth of trout has been investigated by determining the mean length attained at the end of each year of life. To do this, it was necessary first to fix a mean date of hatching, which would represent the beginning of life. The rate of development of salmonid embryos is strongly influenced by temperature (Hayes, 1949) which would vary under natural conditions during

the development period. Stuart (1953) found that under natural conditions in Scottish streams ova hatched early in March after a mild winter, and later in the month after a very cold winter. Spawning in these Scottish streams as in the Llyn Tegid area occurred in October and November so it can be assumed that in the Welsh streams, too, most alevins hatch in March. To determine the mean length of Llyn Tegid trout at the end of each year of life, the mean length for age of trout in the combined January, February and March lake samples of both years has therefore been calculated. The combination of lengths from fish caught during these three months is justified since little or no growth occurs at this time (§ 4, A B). Since the winter band on the scale used in the back-calculation of lengths, is completed in March–May in most Llyn Tegid trout when summer rings start to be formed (Table 6), these mean lengths based on measurements can be compared with the mean lengths based on back-calculation presented by other workers. The mean lengths for the combined January, February and March samples of 1953 and 1954 are given in Table 9. The differences between male and female trout are not significant (at age IV, $t=1{\cdot}21$, $p>0{\cdot}1$), and the sexes will not be considered separately.

TABLE 9

Mean lengths for age of trout in the combined samples for January, February and March 1953 and 1954. Number of fish in brackets.

Age	Mean lengths (mm.) All fish	Males	Females
I	91 (19)	88 (6)	93 (13)
II	153 (72)	147 (16)	155 (33)
III	217 (142)	225 (37)	222 (85)
IV	266 (78)	258 (22)	267 (46)
V	306 (16)	311 (3)	318 (10)

(a) *Growth in Llyn Tegid compared with other lakes*

In Fig. 9 a growth-curve for Llyn Tegid trout, based on Table 10, is compared with growth curves for three lakes in the English Lake District and for Lough Derg in Ireland. The curve for Windermere is taken from Allen (1938) those for Ullswater and Haweswater from Swynnerton and Worthington (1939) and the data for Lough Derg from Southern (1935). In each case, the mean length at hatching has been taken as 20 mm.

Growth in the first three years of life

The most striking difference between Llyn Tegid trout and trout from the other lakes is the much poorer first-year growth and the subsequent acceleration of growth of the Lake District and Irish fish in contrast to the almost straight-line growth of Llyn Tegid trout from hatching to age III. It seemed possible that this difference was due to the effect of Lee's phenomenon (Lee, 1912) in the back-calculated lengths of the Lake District and Irish fish. This phenomenon results in a decrease in the back-calculated lengths for a particular age with the age of the fish whose scales are used in making the calculation. If the calculated lengths at age I are more strongly affected than those for later years, then the mean calculated length at age I would be relatively more depressed than those for subsequent ages, producing a flexion in the growth

curve at age I. Examination of the mean of measured lengths of one-year-old Windermere trout indicated that this was the correct explanation. Allen (1938) caught sixteen one-year-old fish in Windermere, which had a mean length of 80 mm.; his mean back-calculated length for this age was 54 mm., and he regarded this as being the true mean length of the yearlings, the discrepancy between this and the mean of his measured lengths being the result of net selection and migration effect. However 80 mm. is of the same order as the

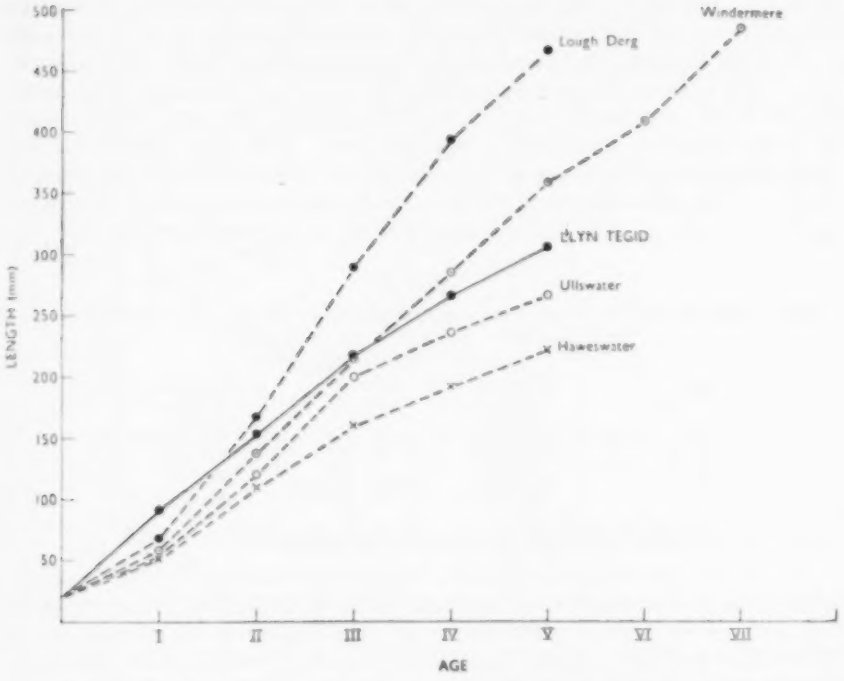

Fig. 9.—Annual growth curves for trout in Llyn Tegid and other British lakes.

measured mean length of one-year-old trout in the Afon Lliw (89 mm.) which suggests that the discrepancy found by Allen was due not to net selection or migration effects but rather to the method of back-calculation. To decide if this was so, a growth curve was constructed for Llyn Tegid trout based on back-calculated lengths ; it closely resembled the curve for Ullswater (Ball, 1957). It can be concluded therefore that the inflection in the Lake District and Irish curves at age I, like that in the Llyn Tegid back-calculated curve, is an artefact due to the influence of Lee's phenomenon on back-calculated lengths, and that true growth curves for Lake District and Lough Derg fish, based on measured lengths, would be nearly straight lines from 0 to III, resembling the true growth curves for Llyn Tegid trout.

The different slopes of the back-calculated curves must reflect real dif-

ferences in growth rate in the second and third years, since all the curves will be subject to the same errors of method. Thus, up to age III Lough Derg trout grow fastest, followed by Windermere trout, Ullswater and Llyn Tegid trout, and Haweswater trout.

Growth in the fourth and subsequent years

In the case of Lake District trout, the calculated mean lengths of three, four, and five-year-old trout are very similar to the measured mean lengths of fish of these ages (Table 10). Hence, the flexion in the general growth curves for Ullswater and Haweswater trout at three-years-old (Fig. 9) must indicate a real reduction in the rate of growth and cannot be due to the defi-

TABLE 10

Measured (M) and back-calculated (BC) lengths of Lake District trout. Data from Swynnerton and Worthington (1939) and Allen (1938). Number of fish in brackets.

Mean lengths in mm.

Age	Haweswater		Ullswater		Windermere	
	M	BC	M	BC	M	BC
III	167 (29)	160 (60)	212 (24)	200 (67)	217 (174)	215 (243)
IV	192 (26)	192 (31)	242 (30)	236 (43)	283 (54)	285 (69)
V	222 (5)	222 (5)	266 (13)	266 (13)	358 (9)	358 (15)

ciencies of the back-calculation method. A similar, though less marked, reduction in growth rate occurs in Llyn Tegid trout at the same age. In contrast, Windermere and Lough Derg trout continue steady growth, at least until five-years-old (Fig. 9). Swynnerton & Worthington (1939) discussing this difference between Haweswater and Ullswater on the one hand and Windermere and Lough Derg on the other, emphasized the absence of pike in the first two lakes and the presence of pike in the last two, suggesting that since pike eat trout (Allen, 1939), the numbers of older trout competing for food will be reduced and the survivors grow more rapidly when pike are present than in pike-free waters. This simple explanation will not hold for Llyn Tegid which contains pike and shows a decline in the trout growth rate after age III.

On the basis of the mean size attained by five-year-old trout, the lakes can be arranged in the following order of decreasing growth-rate : Lough Derg–Windermere, Llyn Tegid–Ullswater–Haweswater.

(b) *Annual growth in the lake and neighbouring streams*

Figure 10 shows growth curves for Llyn Tegid, two tributary streams the Lliw and Glyn, and two moorland streams the Upper Lliw and Rhydwen.

Mean lengths for the Lliw are based on samples taken in October 1953 and February and March 1954. Since there is little or no growth in the period October–March (§ 4 A) the combination of these samples to give mean lengths at the end of each year of life is justified. The same consideration justifies the use of mean lengths from the September Rhydwen samples as mean lengths at the end of each year of life, and the similar use of mean lengths of fish caught in the Upper Lliw in October 1953. The Glyn figures are based on fish caught during the summer growth period, in June 1953, May 1954, and August 1954. They have been plotted in Fig. 10 as if obtained from fish

caught at the beginning of July, the average of their actual dates of capture.

(i) *The lake and tributary streams*

Figure 10 shows that growth is better in the lake than in the two tributaries. One-year-old fish have approximately the same length whether caught in the lake, the Glyn or the Lliw. One would expect this, since the earliest migrants to the lake (the one-year-old fish actually caught in the lake) enter during their first winter, having spent their first summer in the tributaries, when most of

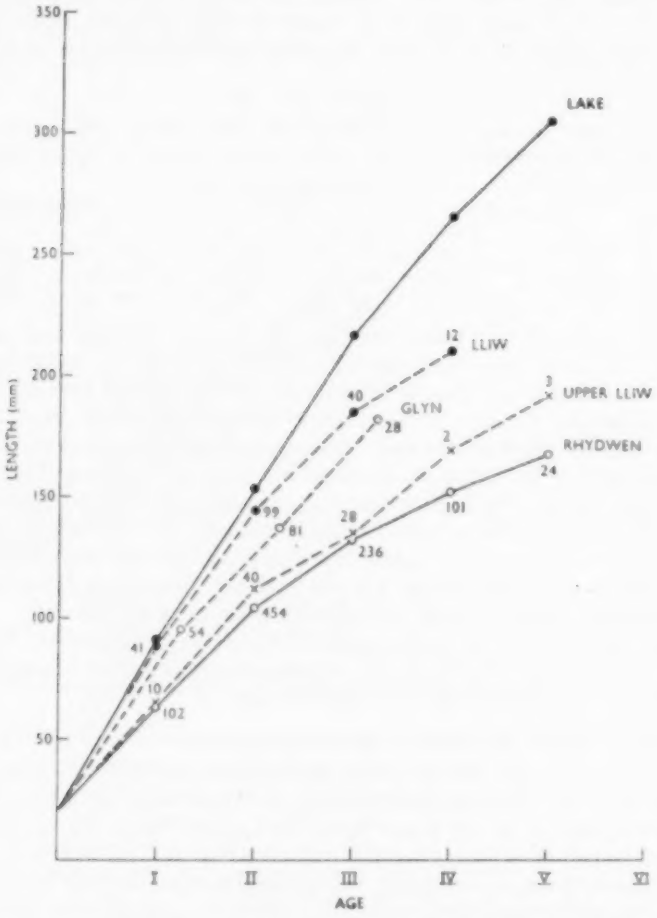

Fig. 10.—Annual growth curves for trout in Llyn Tegid and neighbouring streams.

their first-year growth would be completed. Two-year-old lake trout are decidedly longer than stream fish of the same age (Fig. 10). Some of these lake fish will be 2-winter migrants, with a mean length slightly greater than

that of their contemporaries remaining in the stream (Fig. 11 ; Ball & Jones, 1960). The other two-year-old lake fish are 1-migrants, which, having already spent a summer in the lake, have grown more rapidly than fish in the tributary streams. Figure 11 shows how the growth-rate of migrant trout is increased

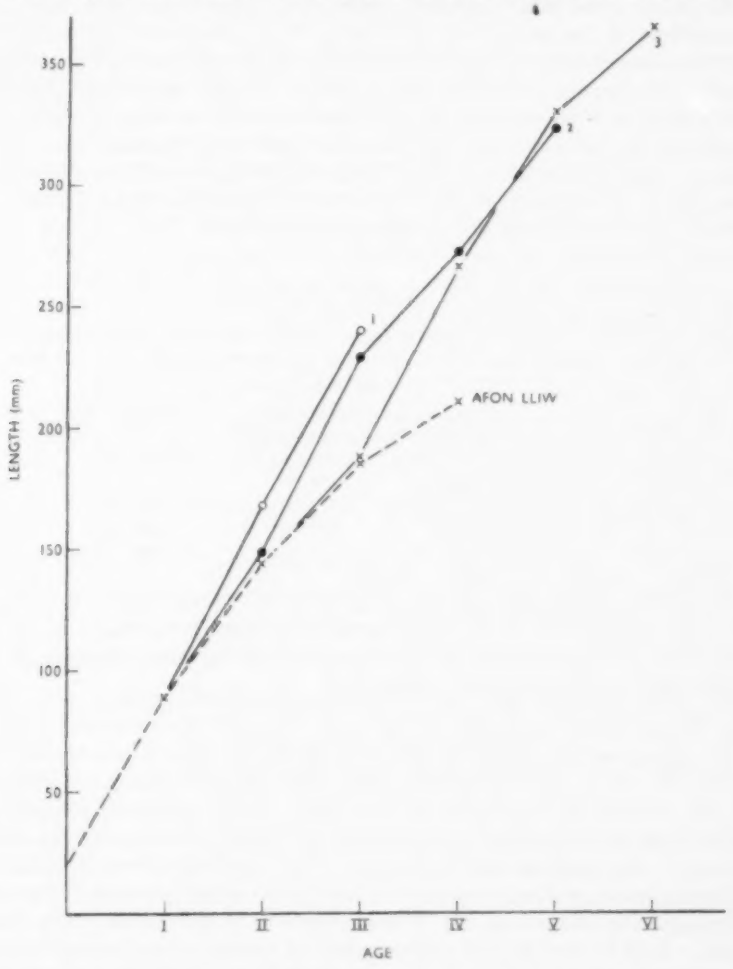

Fig. 11.—Growth curves for different migrant groups (1, 2 and 3) in the lake, compared with the growth of trout in Afon Lliw. Based on Table 11.

after they move into the lake, and how the mean length of three-year-old lake trout given in Fig. 10 is based on samples which include 2 and 1-migrants which have respectively spent one and two summers in the lake and so are much bigger than the newly-arrived 3-migrants of the same age.

The growth-rate of trout in tributary streams declines with age more

rapidly than that of trout living in the lake (Fig. 10), indicating that the lake offers better conditions for trout growth than the streams. The same conclusion follows from the improvement in growth shown by trout on migrating to the lake from tributary streams (Fig. 11), an improvement which is reflected on the scales (Ball, 1957; Ball & Jones, 1960). Just what are the factors responsible for the better growth in the lake cannot yet be decided. It is likely that trout have more living space in the lake and more food, including, probably, larger food organisms than in the streams. Living space might influence growth either via its effect on competition for food or more directly by its influence on appetite and the efficiency of utilisation of ingested food (Brown, 1946). Crowding may also modify the stability of the social size hierarchies which appear to influence the growth rate, the hierarchies being probably less stable in overcrowded conditions (Brown, *op. cit.*).

TABLE 11

Mean lengths (based on measurements) of fish of different migrant groups. Number of fish in brackets. Based on the January, February and March samples, 1953 and 1954.

Age	Mean lengths (mm.)		
	1-migrants	2-migrants	3-migrants
I	As for trout in Afon Lliw—89 (42)		As for Afon Lliw
II	168 (20)	149 (52)	144 (99)
III	240 (9)	229 (84)	188 (41)
IV	—	272 (19)	267 (52)
V	—	323 (5)	330 (4)
VI	—	—	365 (1)

The annual growth rate appears to be similar in the Lliw and Glyn (Fig. 10). The discrepancy at age II probably results from the Glyn samples being taken after the big spring migration of the larger fish to the lake, whereas the Lliw samples were taken before this migration.

(ii) *Tributary and moorland streams*

The growth rate in moorland streams is strikingly less than in the tributary streams (Fig. 10). This difference is shown by the first-year mean lengths, so that the factors responsible for slower growth in the moorland streams must operate from the beginning of life. These factors are not known for certain, but one or two possibilities are known. The moorland streams carry large numbers of trout, and are very much overcrowded compared with the tributary streams and the lake, which may influence growth as mentioned in the previous section. It is known, too, that the moorland trout becomes sexually mature at a younger age than trout in the lake and tributary streams (Ball, 1957). This may influence growth in two ways :

(i) Sexual maturation in fishes is generally followed by a reduction in growth rate (Fage & Veillet, 1938).

(ii) The size of ova tends to increase with the size of the parent trout, and larger ova tend to produce larger alevins with an intrinsically higher growth rate than the smaller alevins from smaller ova (Dahl, 1919). Dahl (*op. cit.*)

showed that this influence of egg size on growth rate was operative throughout the individual life, and Higgs (1942) subsequently showed that it operated for at least seven months in Kamloops trout (*Salmo gairdnerii kamloops*). Most of the mature female fish in the moorland streams will be much smaller than those in the tributaries, producing smaller eggs and consequently slower-growing progeny. On the other hand, Rodd (1946) has brought forward evidence indicating that environmental factors can easily outweigh initial differences in the size of eggs and fry. In addition, of course, there may be genetically determined differences in growth rate such as those demonstrated in lake and stream trout in Sweden by Alm (1939). The age at which sexual maturity is attained is probably genetically determined (Alm, 1939, 1949). Alm was, however, able to demonstrate that environmental influences are more important than genetic effects in producing the different growth rates, and the effect of overcrowding on the food supply in the moorland streams is an obvious subject for further investigation. Jones (1956) has emphasized the likelihood of a shortage of larger food animals in limiting the growth of fish in the Rhydwen.

TABLE 12

Mean lengths in each year of life and annual mean specific growth rates for the different migrant groups in the lake.

Age	Mean lengths (mm.) and mean annual specific growth rates (% length per annum)					
	1-migrants		2-migrants		3-migrants	
I–II	130 mm.	61%	—	—	—	—
II–III	204 mm.	36%	189 mm.	43%	—	—
III–IV	—	—	251 mm.	17%	228 mm.	35%
IV–V	—	—	298 mm.	17%	348 mm.	10%

(c) *Specific growth rate*

The rate of growth is often conveniently expressed as the specific, instantaneous or geometric growth rate :

$$G = \frac{\log_e L_2 - \log_e L_1}{T_2 - T_1} \times 100$$

where L_2 and L_1 are the lengths (or weights) at times T_2 and T_1 respectively, and G is the specific growth rate as the percentage increase per unit time. In studying annual growth, L_1 and L_2 are the lengths (or weights) at the beginning and end of each year of life, so T_2–T_1 is one year and G is expressed as percentage length (or weight) per annum.

Figure 12 shows the changes in the specific growth rate in length with age in the lake and streams. Two points stand out : the specific growth rate is higher throughout life in the lake than in the streams, and although there is a marked difference in the first year growth of moorland and tributary stream fish, the subsequent growth rates are nearly the same in all the streams. Thus the difference in growth rates during the first year is of great importance in producing the subsequent size differences of trout in the two types of streams, a conclusion also reached by Frost (1945) in connection with the different

growth of trout in acid and alkaline waters. However, the growth rates of fish of the same *size* are very different in the two types of stream, since, age-for-age, moorland fish are much smaller than tributary stream fish. The curves in Fig. 13 have been constructed by plotting the specific growth rate in each year of life against the mean length in that year, and show clearly that although

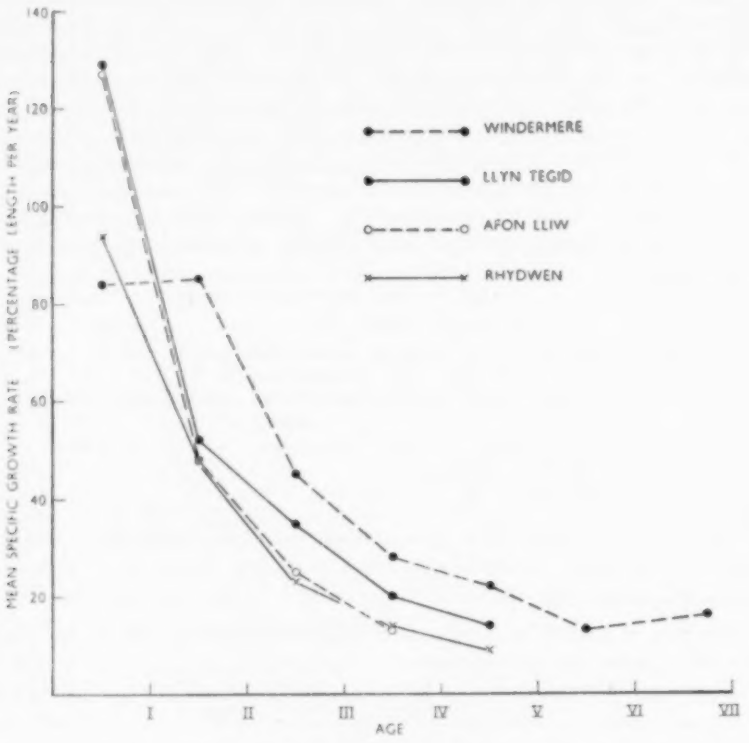

Fig. 12.—Changes in the specific growth-rate with age.

fish of the same age grow at the same rate in both the Rhydwen and the Afon Lliw, fish the same size do not. There is evidence from the growth rates of different migrant groups in the lake (Table 12) that under the same conditions, smaller trout grow faster than larger fish of the same age. In the moorland streams, we find small fish growing at the same rate as much larger fish of the same age in tributary streams. It follows, again, that the two types of stream do not offer identical conditions for trout growth, or that there are genetic differences between the fish in the two types of stream ; or, most probably, both possibilities may apply.

The curves in Fig. 12 illustrate two generalisations concerning animal growth originally made by Minot and summarised by Medawar (1945) : the

specific growth rate declines with age, and its negative acceleration decreases with age. Table 12 suggests that the specific growth rate of trout decreases with increasing size independently of age. It seems possible therefore that the observed decline in specific growth rate with age is at least partly a function of increasing size rather than solely the result of physiological changes in the ageing tissues.

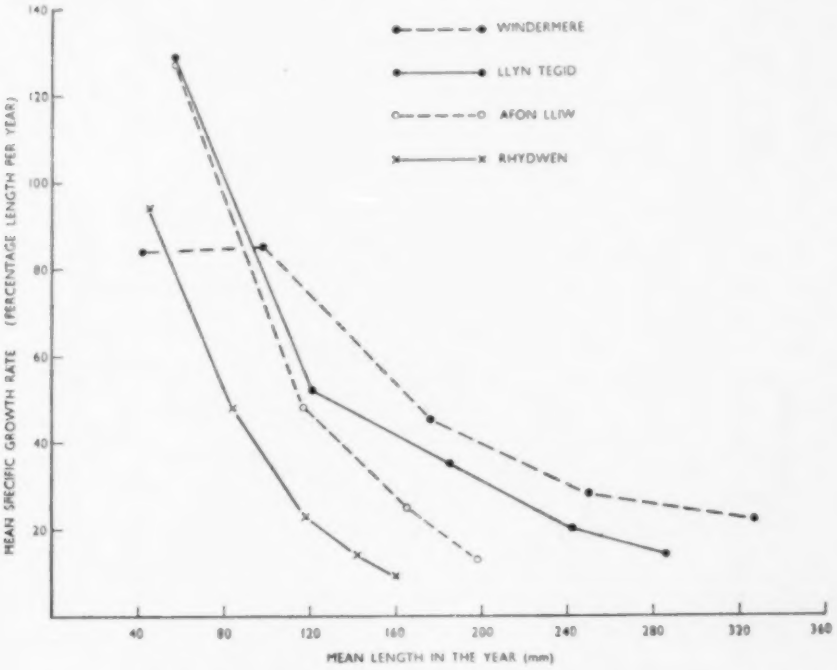

Fig. 13.—Changes in the specific growth rate with size.

(d) *Growth in the streams compared with other rivers*

Figure 14 presents growth curves for two stations on an Irish river, the Liffey (Went & Frost, 1942) and two on a Scottish stream, the River Forss, Caithness (Frost, 1950.) These workers used the back-calculation method which is responsible for the differences in shape in the first two years between these curves and the curves for the Rhydwen and Lliw.

In the River Liffey survey of brown trout growth, Balysumttan was chosen as a station where the water was acid and trout growth poor, and Straffan as a station with alkaline water and quickly-growing trout (Frost, 1945). Taking growth at these stations as standards, Lliw trout can be said to grow moderately well and Rhydwen trout very badly. Frost (1950) in discussing her results for growth in the River Forss pointed out the association between waters deficient in bases and poor trout growth, and those rich in bases and good trout growth. However, large trout have been found in acid (humic)

waters (Frost, 1945) and the direct effect of calcium ions on growth which has often been postulated, seems disproved by the results in the *Salmon and Freshwater Fisheries Report* (1936) and those obtained by Wingfield (1940), which showed that the removal and addition of calcium ions to the water did not

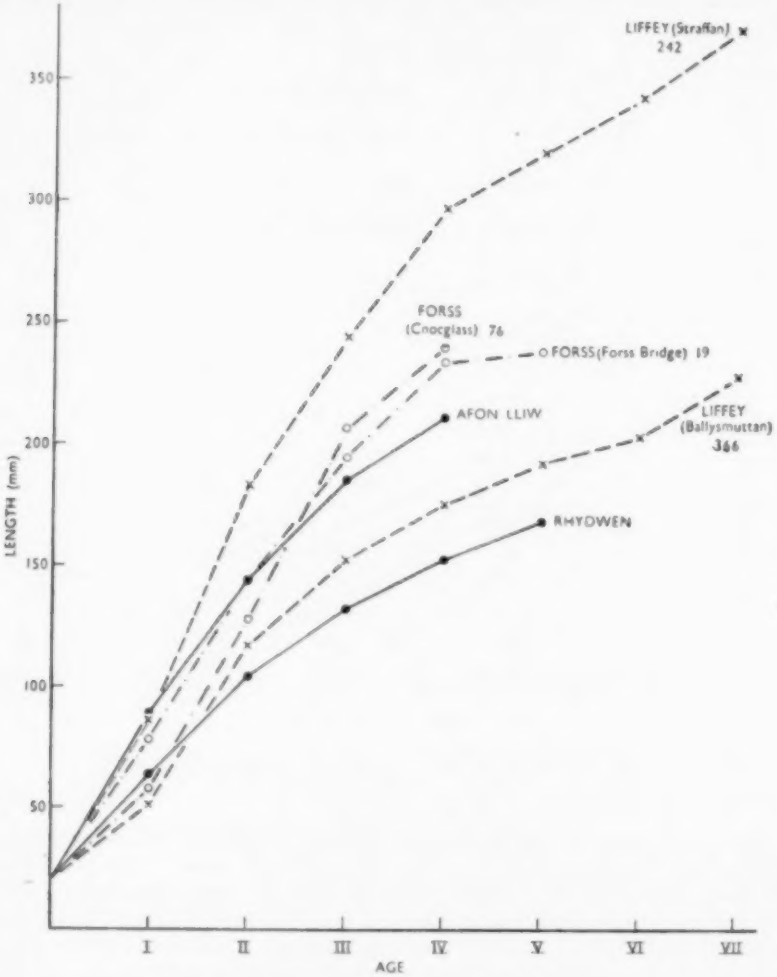

Fig. 14.—Growth curves for different rivers.

produce changes in the growth rate of yearling trout. It is, however, possible that the chemical composition of the water may influence growth by acting directly on the early growth of alevins and fry.

Both the Lliw and the Rhydwen are as poor in bases as the Liffey at Balysmuttan : total hardness as $CaCO_3$ was 5·0–14·3 mg/litres at Balysmuttan 5·9 mg/litre in the Lliw and 7·3 mg/litre in the Rhydwen. Other factors, such

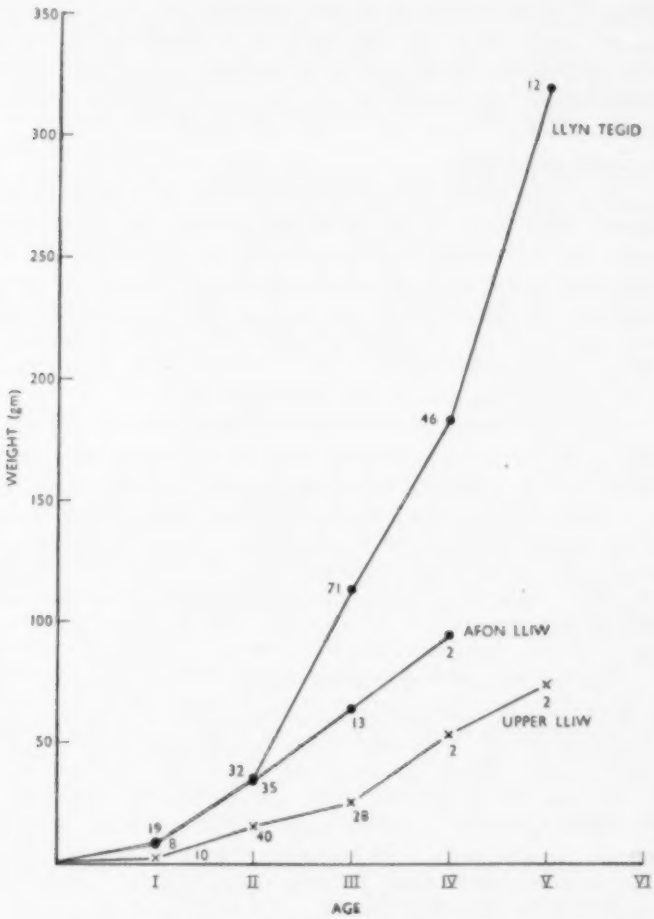

Fig. 15.—Annual growth curves (weight) for trout in Llyn Tegid and tributary streams.

as food supply, space, temperature and genetic differences must be responsible for the wide differences in growth rates in these streams.

2. *Growth in weight*

For the lake trout the mean weights for age of fish caught in January, February and March 1954 have been taken as the mean weights at the end of each year of life. For Afon Lliw trout corresponding figures were obtained from the February and March 1954 samples, and from the December 1953 samples from the Upper Lliw. The results are shown as growth curves in Fig. 15 and call for little comment. Growth in weight in the lake is much faster than in the Upper Lliw, with growth in the Lliw falling off to an intermediate level after the second year. Yearling trout are lighter, as well as

shorter in the moorland stream than in the tributary. Curves for the specific growth rate in weight (Ball, 1957) like those for the linear specific growth rate (Fig. 12) indicate the probable importance of different growth rates in the first year in determining subsequent differences in the size of moorland and tributary stream trout.

3. *Length-weight relationship*

The length-weight relationship of the trout has been studied by plotting the logarithms of the mean length at the end of each year of life against the logarithm of the corresponding mean weight (Fig. 6). Results from the Upper Lliw, Afon Lliw and the lake are available and they all lie in a straight line, indicating no fundamental change in the length/weight relationship with age or locality amongst the age groups sampled (O + to IV +). The regression line, fitted by eye, has the equation

$$\log \text{weight} = 2{\cdot}93 \log (\text{length}) - 4{\cdot}8$$
$$\text{or weight} = 1{\cdot}549 \times 10^{-5} (\text{length})^{2{\cdot}93}$$

The first point for the Upper Afon Lliw lies below the regression line in Fig. 6. This could be interpreted as meaning that these fish, nearly one-year-old, were in poor condition compared with the fish represented by the other points in the diagram. However, for fish of this small size, weighing errors could be considerable and this, together with the small size of the sample (ten fish) makes it inadvisable to read any significance into the low length-weight ratio of these fish.

5. CONCLUSIONS

Rapid scale growth has been shown to be confined to the period April-October for the majority of the lake trout, though starting in February-March in some individuals. Rapid growth of the body is also confined to the same period. An association between scale growth and body growth is to be expected. Nothing in the literature suggests that scales can grow when the body does not, or vice versa, and Dannevig (1925), Thompson (1926, 1929), Duff (1929), Graham (1929), Gray & Setna (1931), Bhatia (1932) and Jones (1949), have all shown that the formation of wide scale rings (indicating rapid scale growth) corresponds to fast linear growth of the body in various fishes. Van Oosten (1957), in a review of the use of scales in life history studies, concludes " in many species, the distance between the circuli (rings) varies with the intensity of (body) growth. In such instances when growth also slows down, the circuli become weak and discontinuous ". It can be considered, therefore, that the formation of wide rings on the scales of an individual trout indicates that the body is growing quickly. This has an important consequence in that conclusions reached concerning seasonal scale-growth, based on examination of scales, can be extended to describe the seasonal linear growth of the body. The exact beginning and end of the growing season cannot be fixed with certainty from growth curves and length-frequency histograms, but can be fixed by reference to the picture of scale growth that has resulted from study of the scales month-by-month.

By combining the results from the scale studies, growth curves and length-

frequency histograms, the following account of the growth of Llyn Tegid trout over one-year-old emerges :

1. During the summer months June, July and August, all trout are growing rapidly, adding wide rings to the scale edge at a rate of two or three a month. Two-year-old trout during this time have a mean specific growth rate of 0·3 per cent length per day.

2. Starting in August and continuing into September-October narrow summer rings are formed at the same rate as the ordinary summer rings. The growth rate of the scales must therefore be reduced at this time. The present data for body growth do not show whether or not there is a retardation of body growth at this time; such a retardation was found in salmon parr by Allen (1940, 1941) and Jones (1949), and its occurrence in trout seems highly likely.

3. In September the formation of narrow (winter) rings starts in 30 to 40 per cent of the fish, and by October 50 to 70 per cent show this type of scale growth. This is probably paralleled by an extreme retardation of body growth, but this cannot be demonstrated by the present data.

4. A few trout, less than 10 per cent of the total, continue scale growth (and probably body growth) at the reduced summer rate at least until October when they probably stop growth without forming narrow rings.

5. About three-quarters of those trout which form narrow rings in September (20 to 30 per cent of the total) resume rapid scale growth in September and early October, forming an average of three wide rings. They stop scale growth at the end of October. Resumption of body growth parallel to this scale growth is highly likely, but cannot be demonstrated with the data to hand.

6. Scale structure, growth curves and length-frequency histograms indicate that there is no growth from October to February. In scale samples taken during this period, 30 per cent of the fish appear to be growing at a " summer " rate, the rest at a " winter " rate, but in fact none are growing at all. This conclusion recalls the findings of van Oosten (1923, 1929) and van Oosten & Hile (1949) on scale growth of coregonids, and Duff (1929) on the scale and body growth of cod.

7. Rapid growth is resumed by 25 to 30 per cent of the trout in February-March. This figure is derived from the following considerations :

(a) The decrease of 15 per cent in the number of slow growers from February to March 1954.

(b) In the case of early growers with three or more marginal wide rings, the mean number of marginal rings increased significantly from February to March 1954. The percentage of trout in this condition did not alter significantly at this time. Hence these fish, 10 per cent of the total, must have resumed rapid growth in February-March.

(c) The 11 per cent increase in early growers with one or two marginal wide scale rings in February-March 1954 must have been caused by the resumption of growth by the 15 per cent slow growers referred to in (a) above, the 4 per cent difference resulting from sampling errors.

This gives a total of $15+10=25$ per cent of all trout resuming growth in February-March. It is impossible to decide whether the rest of the early growers, those with one or two marginal wide scale rings, resumed rapid growth at this

time or not. These constitute 10 per cent of the total. Hence one arrives at a maximum figure of 35 per cent and a minimum of 25 per cent of all trout resuming growth in February-March.

8. The proportion of rapidly growing fish then increases each month at 100 per cent in June, July, August.

9. Younger trout tend to start growth in spring earlier than older individuals.

10. Trout in Llyn Tegid grow faster than those in Ullswater but slower than Windermere trout. As in Haweswater and Ullswater, growth falls off after age III, in contrast to trout in Windermere and Lough Derg in which the growth curve is a straight line to age V at least.

11. Growth in the tributary streams is slower than in the lake but better than in the moorland streams. First year growth is markedly poorer in the moorland streams. Compared with Went and Frost's (1942) results for River Liffey trout, growth in the tributary streams is moderately good, growth in the moorland streams is very poor.

12. In all streams and in the lake, the mean annual specific growth rate declines with age, and its negative acceleration decreases with age. The decline in growth rate is reflected by the growing scale, the number of rings in the summer band decreasing with age.

13. Trout show a marked enhancement of growth when they first enter the lake from the tributary streams in which they start life.

14. The logarithmic plot of mean weight against mean length for trout of all sizes and in all types of localities studied is a straight line having the formula

$$\text{weight} = 1{\cdot}549 \times 10^{-5}\ (\text{length})^{2.92}$$

Hence the condition factor $K = \dfrac{\text{weight}\ 10^4}{\text{length}^3}$ can be used to compare the condition of trout of different sizes.

15. The condition of the non-spawning lake trout is poor during the winter, rises to a maximum in April-June and declines to the winter level in September. There is a slight rise in condition to a winter peak in December, followed by a decline to the lowest value in March before the steep rise in condition in spring. These seasonal changes in conditions are correlated with the amount of fat stored around the stomach and pyloric caeca, the principal food reserve of trout. The value of K decreases slightly with age.

6. ACKNOWLEDGMENTS

We are grateful to the Welsh Land Sub-Commission which made this work possible by allowing us to catch trout from waters on its Merionethshire estate. Our thanks are also due to Professor R. J. Pumphrey, F.R.S., for valuable advice and criticism, to Miss J. Hughes and Mrs L. Lloyd for technical assistance, and to Mr W. Irvine who took the photographs. For additional help in the field we thank many people, but especially Capt. G. H. A. Boyle, Dr Alexine Tinne, Professor J. D. Craggs and Mr S. W. Drinkwater. During the investigation one of us (J. N. B.) held a D.S.I.R. maintenance grant.

7. SUMMARY

1. The age of Llyn Tegid trout can be reliably determined from the scales

by counting the number of completed winter bands. The winter rings are formed annually in September-October.

2. The seasonal growth pattern of lake trout has been investigated by examination of the scale structure each month and by following the monthly changes in the mean lengths of each year-class. Growth is confined to the period February-March to September-October, no growth taking place during the winter.

3. Annual growth has been studied by determining the mean length of trout at the beginning of each year of life. The mean specific growth rate in the lake and streams declines with age and its negative acceleration decreases with age. Growth in Llyn Tegid and the neighbouring streams has been compared with growth in other British waters.

4. Growth in the tributary streams is better than in the moorland streams but poorer than in the lake. Trout show an increase in growth rate when they migrate from the tributary streams to the lake.

5. The length-weight relationship is the same for trout of all ages and in all the localities studied.

6. Seasonal changes in the usual condition factor, $K = \frac{\text{weight } 10^4}{\text{length}^3}$ have been determined. K is correlated with the amount of reserve fat stored around the stomach and pyloric caeca.

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A

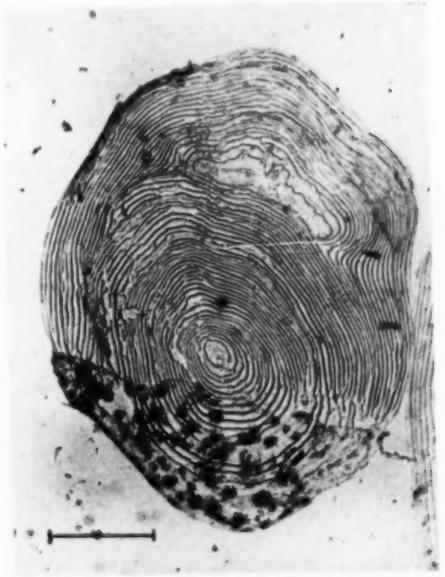
B

C

D

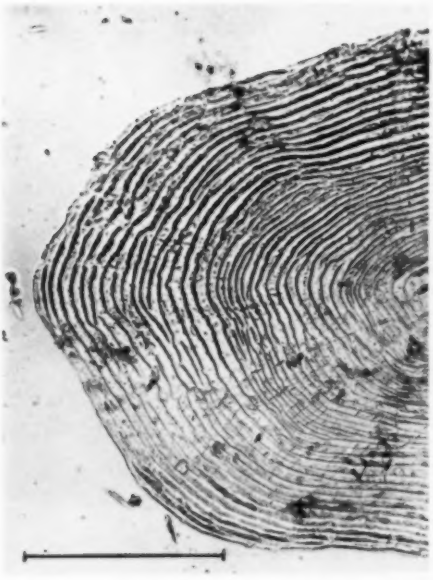
Scale structure. Scale = 0.5 mm. (For further details see text pp. 8-9.)

A



B

Accident Scales. Scale 0·5 mm. (See page 9.)



A

B

C

D

Scales taken on different occasions from a single tagged fish. Scale—0·5 mm. A—9th October 1953. B—21st October 1953. C—5th January 1954. D—9th March 1954.

THE ASSOCIATION BETWEEN THE HERMIT CRAB *EUPAGURUS BERNHARDUS* (L.) AND THE SEA ANEMONE *CALLIACTIS PARASITICA* (COUCH)

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[Accepted 14th April 1959]

(With 2 plates)

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INTRODUCTION

The associations between various hermit crabs and sea anemones have long interested field naturalists and students of animal behaviour. About a century ago, Johnston (1847) and Gosse (1860) summarised the known facts of the occurrence of the cloak anemone (*Adamsia palliata*) and the parasitic anemone (*Calliactis parasitica*) in British waters. Subsequent experimental observations on these anemones were mostly confined, however, to Mediterranean forms. Faurot (1910 and 1932) working at Banyuls, Brunelli (1910 and 1913) and Brock (1927) working at Naples, described the mutual adaptation of anemone and crab in the two associations, *A. palliata* with *Eupagurus prideauxi* and *C. parasitica* with *Pagurus striatus* (Banyuls) and with *P. arrosor* (Naples). They also elucidated the respective roles of crab and anemone in establishing and maintaining the associations and discussed the advantages which each partner obtained from the association in each case.

The observations of Faurot and Brunelli in particular have been incorporated into general and popular accounts as the standard patterns of hermit crab—sea anemone association. *Adamsia* and its crab form an association that is truly symbiotic. The two species are mutually adapted to each other to such an extent that they cannot live apart successfully. The active role of the crab and the co-operative behaviour of the anemone in establishing the partnership were clearly demonstrated. There is no reason to doubt that these observations apply to the cloak anemones in British waters so they need not be referred to again in this paper.

The associations between *C. parasitica* and its hermit crabs, *P. striatus*, *P. arrosor* and *E. bernhardus*, are more casual and were regarded by Faurot (1910) as an example of mutualism. In this case there are no specific mutual adaptations of a structural kind and apparently, the two species can live apart without suffering any obvious disadvantages. Yet they are usually found living together in nature and there are significant mutual adaptations in the behaviour of both crab and anemone which contribute to the maintenance of the association. All these workers are agreed in ascribing an active role to the crabs, *P. striatus* and *P. arrosor*, in placing the anemone on the shell. *Calliactis* attached to other objects or other shells are approached by *P. arrosor* and stroked or prodded until they become detached and then they may be carried and held against the shell until they adhere (Brunelli, 1913 and Brock, 1927). Faurot (1910 and 1932) describes similar behaviour in *P. striatus* but he states that the anemone, when it has been stimulated by the stroking movements of the crab, frees its pedal disc from the surface to which it has been attached and then proceeds to attach itself to the shell in a characteristic way. First the tentacles stick to the shell, then the oral disc becomes applied and finally, the pedal disc is swung up by a somersaulting movement to take up its position on the shell close to the place occupied by the oral disc. A *Calliactis* that is not fixed, but lies, say, on the bottom of a container, will attach itself to a shell in exactly the same way, without the crab being involved at all.

My interest in this problem arises from observations made in the course of other work which suggested that the familiar accounts which ascribe an important role to the crab in establishing the association might not be true of *E. bernhardus* and *C. parasitica* in British waters. For this reason, and because the earlier papers included almost no quantitative data, it seemed desirable to carry out a certain number of new experiments on the association of these two animals, and to support an account of the observations with a photographic record. Indeed, by the standards of present-day treatments of behaviour patterns of this kind, all this earlier work is inadequate. Full photographic and film records of these interesting phenomena would be required nowadays as proof of the correctness of the observations. Data would also be required on the performances of certain numbers of animals under definite conditions as evidence that the phenomena are a general and normal feature in the lives of these animals. This paper describes an attempt to approach the problem in these ways.

PRELIMINARY OBSERVATIONS

Calliactis parasitica shows no special adaptations of its pedal disc, either in shape or structure, for attachment to the shells of *Buccinum* inhabited by *E. bernhardus*, on which it is usually found in Plymouth waters. It can and does adhere, as Faurot pointed out, to stones and other objects on the sea bottom but it is never found on shells inhabited by living *Buccinum*.

The attachment of *Calliactis*, which have been removed from shells, to stones, glass plates and other objects, is in no way remarkable. An animal lying on its side, or supported in some way, merely secures a foothold by the

edge of the pedal disc, and from this foothold the attachment spreads until the whole surface is adherent. The entire process may take many hours and is accomplished by the combined effects of muscular suction and cementing secretions. Essentially this process is the same as the method employed by *Actinia equina* and *Anemonia sulcata*. Compared with these, however, the pedal disc of *Calliactis* attaches much more slowly, but once the attachment is made, it is firmer and because the attached foot is virtually immobile, it is more permanent.

The attachment of an unattached *Calliactis* to a shell occupied by *E. bernhardus* is very different indeed. Faurot (1910 and 1932) described this briefly and the following expanded account based on my own observations, agrees with his in the essential points. First, the tentacles explore the surface of the shell very actively and many of them adhere to the shell, perhaps by glutinant nematocysts, forming an attachment firm enough to hold the anemone on the shell even when the crab moves about. This tentacular attachment develops within a few minutes into a firmer attachment in which the whole oral disc is involved as well. Apparently, the radial musculature contracts and pulls against the expanded margin and its adhering tentacles and so produces an immense suctorial disc. At no other time does the animal seem so much to deserve its specific name '*parasitica*'. Once this is achieved, the anemone is virtually safe from being dislodged, even by the most active movements of the crab.

All this may take 5 to 10 minutes and is followed at once by a slow bending of the column which, in another few minutes, brings the pedal disc up to the shell so that the animal is bent double. The pedal disc, meanwhile, becomes greatly distended and begins to adhere to the shell immediately contact is established. Within another few minutes the whole pedal disc has spread out, its swollen surface and edge becoming bedded down firmly to fit the grooved, often encrusted, surface of the shell. Finally, when the pedal disc is firmly attached, the tentacles and oral disc let go and in the space of another 2 to 3 minutes, the column straightens out and the animal assumes its normal extended posture.

Faurot (1910) described this process briefly as the final stage in a series of responses produced in *Calliactis* by the palpations of the crab. He does not suggest that the anemone can perform this complicated manoeuvre, first detaching itself from the object to which it is attached and then climbing on to the shell, without preliminary stimulation by the crab. The experience of my preliminary observations suggested, however, that with shells occupied by *E. bernhardus*, the crab plays little or no part in the process. The anemone deserts a position to which it has been attached under the stimulus of contact with a crab or its shell. I did not observe any examples of behaviour in this crab which seemed to contribute in any way to the relaxation of the hold of the pedal disc on stones or glass plates or other shells to which anemones had previously become attached. This enhanced the significance of the behaviour pattern exhibited by *Calliactis* in relation to this association, which is surely one of the most remarkable to be found in any of the normally sessile coelenterate animals. It is surprising that it aroused so little comment, either by

Faurot himself, or by later workers, but it has always been assumed, especially from the work with *Pagurus arrosor* where the anemone appears to be entirely passive (Brunelli, 1913 ; Brock, 1927), that the behaviour of the crab was the more remarkable element in the situation. Therefore, it has seemed appropriate to re-describe the behaviour of *Calliactis* in this connection and to illustrate it with the photographs in Plates 1 and 2 which show most of the stages mentioned in the account given above.

EXPERIMENTS AND RESULTS

The preliminary observations having indicated that the anemone is the active partner in this association between *Calliactis parasitica* and *Eupagurus bernhardus*, three experiments were designed to test this impression and to provide data on a number of specific points. The experiments and the results in each case will now be described in turn.

Experiment A

In each of twelve containers (" Brefitts ") fitted with running sea water, four identifiable *C. parasitica* (a, b, c, d) were introduced and allowed to settle on the walls or floor. About 24 hours later, *E. bernhardus* labelled 1 to 12 were introduced, one in each of the containers. Subsequent events were followed visually and records taken of the numbers of anemones attaching or attached to the shells occupied by the crabs. This experiment was repeated with the same crabs a number of times. Later, empty shells were introduced and the numbers of attachments recorded in the same way.

The summarised results of this experiment are given in Table 1. Each trial was continued for 20 to 30 hours. During the first few hours, a number of anemones quickly became attached but after 20 hours, very few further attachments were made and the trial was discontinued. The anemones were then removed from the shells, the crabs were taken out of the containers and the anemones allowed to settle on the glass again before another trial was begun.

The time table of settling on shells followed a fairly standard pattern in all the trials. Trial 1 provides a typical example : of the forty-eight *Calliactis*, eight were on the shells after 2 hours, thirteen after 3 hours, fifteen after

TABLE 1

Migration of *Calliactis* from surface of glass containers to occupied and unoccupied shells. (Experiment A. See text for details. Each trial began with all forty-eight *Calliactis* attached to inside surfaces of twelve glass containers. In Trials 1–4, twelve shells with *Eupagurus*, in Trials 5–6, twelve shells without *Eupagurus*, were introduced. Duration of Trials : 20–30 hr.).

Trial	*Calliactis* attached to shells	*Calliactis* remaining attached to glass
1	25	23
2	24	24
3	33	15
4	24	24
5*	26	22
6*	26	22

4 hours, fifteen after 6 hours, nineteen after 9 hours, twenty-four after 16 hours, twenty-five after 29 hours, and twenty-seven after 48 hours. It seemed, therefore, that settling was virtually complete by about 20 hours, and hence the later trials were continued only for that period.

Trials with occupied and unoccupied shells are not strictly comparable because the crabs move about from time to time and this increases the chance of contact between the anemone and the shell. For this reason, in the trials with empty shells, the shells were moved around the vessel several times during the course of the trial. Thus most of the anemones were at some time brought into contact with the shells.

Table 1 shows clearly that under the conditions of this experiment, with the solitary exception of Trial 3, *Calliactis* become attached to empty shells just as readily as to occupied shells. Indeed, all other trials showed a remarkable constancy in the result, with about half the anemones transferring to the shells in every case. We shall see later that there is some tendency for the same anemones to become attached in each trial, but first Experiments B and C will be examined for further information on settling on occupied and unoccupied shells.

Experiment B

In the second experiment, five *Calliactis* with distinctive features or markings were placed in each of three bowls (diameter about 12 inches), together with two stones, a *Pecten* half-shell, and a slate, and allowed to settle on these objects or on the inside surface of the bowl itself. The bowls were covered with netting and immersed in one of the large outdoor tanks at the Plymouth Laboratory. When all the anemones were firmly attached, a shell containing a labelled crab, and another unoccupied *Buccinum* shell were introduced, the empty shell being blocked up to prevent the crab changing from one to the other. Then the netting was replaced and the bowl returned to the tank. The bowl was removed from time to time and any changes in the positions of the anemones were noted.

The results of this experiment are presented in a summarised form in Table 2. In each of the four trials, the observations were continued until the position seemed to be fairly stable, generally about 16 to 24 hours later. The unoccupied shells were moved about from time to time as in Experiment A and for the same reason. At the end of each trial, the anemones were stripped off, the occupied and unoccupied shells were removed, and the anemones allowed to re-settle on the bowl or the other objects before the next trial was begun.

The results of Experiment B are very similar to those of Experiment A. Occupied shells do not acquire anemones more frequently than unoccupied shells. In each trial, about one-half of the anemones migrated from their attachments on the bowl or the other objects, to the occupied or unoccupied shells. The rest showed no such tendency though these were often brought into contact with the shells by the movements of the crab or by the movements of the unoccupied shells mentioned above. Records of the individual performances of the anemones will be considered later.

TABLE 2

Migration of *Calliactis* from various surfaces to occupied and unoccupied shells.

(Experiment B. See text for details. Each trial began with all fifteen *Calliactis* attached to the three bowls or objects contained in them. In all trials, three occupied and three unoccupied shells were introduced. Duration of trials : 24 hr. approx.)

Trial	Occupied shells	Unoccupied shells	*Pecten* shells	Stones	Slates	Bowls
1	4	3	1	0	0	7
2	4	4	1	1	2	3
3	1	4	1	2	4	3
4	4	4	0	1	2	4
Totals	13	15	3	4	8	17

In this experiment, carried out in a deep tank without clear visibility, the behaviour of the crabs could not be followed so closely as in Experiment A. However, nothing suggesting activity by the crab to detach the anemones or to assist their adhesion to the shells was ever observed, either in daylight or at night with the aid of a torch.

Experiment C

In this experiment twenty *Calliactis* were introduced into a large enamelled iron basin (diameter about 24 inches) with sloping sides, on the floor of which stones, *Pecten* shells and slates were scattered. The basin was supplied with running sea water and the anemones were allowed to settle on these objects or on the inner surface of the basin itself. When settling was complete, five shells occupied by *E. bernhardus* and five unoccupied shells (blocked up to prevent crabs moving into them) were introduced into the basin. There was ample space for the crabs to move about the basin but most of the anemones were close to, if not in contact with occupied, or unoccupied shells or both. The crabs moved about fairly actively at first, but within a few minutes they settled down and remained fairly quiet thereafter.

The situation following the introduction of the crabs and the empty shells was watched very closely Within 10 minutes several anemones were already becoming attached to shells in the manner described above. Further attachments of anemones to shells took place subsequently but most of these occurred in the first 2 to 3 hours. After this, migration of anemones from their previous attachments to the shells was infrequent, and after about 12 hours, a fairly stable situation was generally established.

Three trials were performed in this experiment, the anemones being detached at the end of each and allowed to re-settle on the basin or other objects provided, before the occupied and unoccupied shells were introduced again. The results are set out in Table 3.

Table 3 shows that under the conditions of this experiment, *C. parasitica* become attached, if anything, more frequently to unoccupied than to crab-occupied shells. This confirms the experience of Experiments A and B in which no special preference for occupied shells was observed. The close visual

TABLE 3

Migration of *Calliactis* from various surfaces to occupied and unoccupied shells.

(Experiment C. See text for details. Each trial began with all twenty *Calliactis* settled on the basin or on the objects contained in it. In all trials, five occupied and five unoccupied shells were introduced simultaneously. Duration of trials: 18–20 hr.)

Trial	*Calliactis* on occupied shells	*Calliactis* on unoccupied shells	*Calliactis* remaining on stones, *Pecten* shells, basin, etc.
1	6	7	7
2	7	9	4
3	4	10	6
Totals	17	26	17

observations made during Experiment C suggest, however, that under these conditions, where anemones and shells were fairly densely packed, attachment to an unoccupied shell may be easier to achieve than to an occupied shell, simply because it is stationary. On a number of occasions, the movements of the crab were seen to interrupt the complicated manoeuvre by which the anemone first adheres to the shell, sometimes even taking the shell out of reach of the anemone.

Although the crabs were watched very closely in this experiment, only once did a crab display any activity suggestive of the active transplantation of an anemone to its shell. On this single occasion the crab approached a *Calliactis* and seemed to prod it very actively, even pushing one of its walking legs into the stomodaeum. Having done this, it reversed its position so that the shell was brought up close to the anemone which was now immediately behind the crab. The anemone then proceeded to attach itself to the shell in the usual way. The whole sequence of events, however, might have been no more than the movements of a crab changing its position and encountering an attached *Calliactis* as one of the obstacles on the floor of the basin.

The general conclusion from these experiments must be that *Calliactis* is the active member in the establishment of the association with *Eupagurus bernhardus*. In general, the crabs appear to be quite disinterested. On the other hand, empty shells elicit exactly the same pattern of behaviour in *Calliactis* as do the occupied shells, and as the figures obtained under these three different sets of experimental conditions show, no preference for occupied shells is demonstrable.

Individual performances of animals in Experiments A and B

The data provided by Experiments A, B and C are a measure of the tendency for groups of *Calliactis* to desert various surfaces such as glass, plastic, stone, etc., for occupied and unoccupied hermit-crab shells. We have seen that under these experimental conditions from one-half to two-thirds of the animals tend to migrate to the shells. Unattached *Calliactis* probably get on the shells in larger numbers, but *Calliactis* which have been attached to such surfaces for long periods (in these experiments they had been attached for less than 24

TABLE 4

Migration of individual *Calliactis* to occupied and unoccupied shells in Experiment A. (Expanded Table I. See text for details).

Brefitt No.	*Calliactis* identification	Trials with occupied shells				Total No. of attachments		Trials with unoccupied shells		Total No. of attachments	
		1	2	3	4	per anemone	per crab	1	2	per anemone	per shell
1	a	0	0	0	0	0	2	0	0	0	3
	b	0	0	0	0	0		0	0	0	
	c	0	0	0	0	0		0	+	1	
	d	0	+	+	0	2		+	+	2	
2	a	+	+	+	+	4	13	+	+	2	7
	b	+	+	+	+	4		+	+	2	
	c	+	0	+	0	2		0	+	1	
	d	+	0	+	+	3		+	+	2	
3	a	+	+	+	0	3	14	+	+	2	7
	b	+	+	+	+	4		+	+	2	
	c	+	+	+	+	4		+	0	1	
	d	+	+	0	+	3		+	+	2	
4	a	0	0	0	0	0	5	0	0	0	3
	b	0	0	0	0	0		0	0	0	
	c	+	+	+	0	3		+	+	2	
	d	0	+	+	0	2		0	+	1	
5	a	0	0	0	+	1	7	0	+	1	4
	b	0	+	+	+	3		+	0	1	
	c	0	0	0	0	0		0	0	0	
	d	+	+	+	0	3		+	+	2	
6	a	0	+	+	+	3	11	+	0	1	5
	b	+	0	+	0	2		0	0	0	
	c	0	+	+	+	3		+	+	2	
	d	+	+	+	0	3		+	+	2	
7	a	+	+	+	+	4	9	+	+	2	5
	b	+	0	+	0	2		+	+	2	
	c	0	0	+	+	2		0	+	1	
	d	0	0	+	0	1		0	0	0	
8	a	+	0	+	0	2	11	0	0	0	4
	b	+	+	+	+	4		+	+	2	
	c	0	0	+	0	1		0	0	0	
	d	+	+	+	+	4		+	+	2	
9	a	+	0	0	+	2	6	0	0	0	1
	b	+	0	0	0	1		0	0	0	
	c	+	0	+	0	2		0	+	1	
	d	0	0	0	+	1		0	0	0	
10	a	+	0	0	+	2	11	+	0	1	4
	b	+	+	+	+	4		+	+	2	
	c	0	0	+	+	2		0	0	0	
	d	0	+	+	+	3		+	0	1	
11	a	0	+	+	+	3	10	+	+	2	5
	b	+	+	+	0	3		+	0	1	
	c	0	0	0	0	0		0	0	0	
	d	+	+	+	+	4		+	+	2	
12	a	+	0	0	0	1	10	0	0	0	4
	b	+	0	0	+	2		0	+	1	
	c	+	+	+	0	3		+	0	1	
	d	+	+	+	+	4		+	+	2	

Distributions. In four trials with occupied shells numbers of *Calliactis* attaching :

4 times —10
3 „ —13
2 „ —12
1 „ — 6
0 „ — 7

Distributions. In six trials with occupied and unoccupied shells numbers of *Calliactis* attaching :

6 times —9
5 „ —9
4 „ —7
3 „ —6
2 „ —5
1 „ —6
0 „ —6

\+ indicates attachment to a shell.

0 indicates continued attachment to the glass.

TABLE 5

Migration of individual *Calliactis* to occupied and unoccupied shells in Experiment B. (Expanded Table 2. See text for details).

Crab/ Bowl No.	*Calliactis* identification	Object to which anemone attached in trials				Attachments to :		
		1	2	3	4	Crab	Shell	Bowl, Stones etc.
1	a	Bowl	Shell	Slate	Bowl	0	1	3
	b	Crab	Crab	Shell	Stones	2	1	1
	c	Bowl	Stones	Stones	Bowl	0	0	4
	d	Crab	Bowl	Slate	Crab	2	0	2
	e	Bowl	Slate	Slate	Bowl	0	0	4
2	a	Shell	Shell	Shell	Slate	0	3	1
	b	Bowl	Bowl	Slate	Bowl	0	0	4
	c	Crab	Crab	Unattached	Crab	3	0	0
	d	Bowl	Slate	Crab	Crab	2	0	2
	e	Pecten	Crab	Shell	Crab	2	1	1
3	a	Shell	Shell	Shell	Shell	0	4	0
	b	Shell	Shell	Bowl	Shell	0	3	1
	c	Bowl	Pecten/ stones	Slate/ bowl	Shell	0	1	3
	d	Bowl	Crab	Stones	Bowl	1	0	3
	e	Crab	Slate/ bowl	Bowl	Shell	1	1	2

Distributions : Numbers of *Calliactis* attaching to occupied or unoccupied shells in four trials.

4 times —1
3 „ —5
2 „ —3
1 „ —3
0 „ —3

hours) seem less ready to move to shells. No controlled experiments were carried out on these points but these are general impressions from scattered observations.

Experiments A and B also provide information on the records of individual *Calliactis* and individual crabs and shells. Tables 4 and 5 present the individual performances of the anemones in these experiments and show clearly that there were some animals which always became attached to shells and some others which never became attached. If we examine the distribution of the individual anemones by the numbers of times they settled on the shells, we find that it is far removed from a normal distribution. One must conclude that in this population of *Calliactis* there are big individual differences in the strength of the tendency, or the ability, to become attached to the shells presented.

Because the same group of anemones in each container was always offered the same crab or shell, it is not certain whether the individual differences observed relate to the anemones or the shells. Further experiments in which crabs and shells were moved from container to container would probably clarify this matter. However, a comparison of the performances of the anemones with the occupied shells on the one hand, and with the unoccupied shells on the other, suggest that these are differences in individual anemones. It can be seen from Table 4 that those anemones which failed to become attached to the occupied shells also failed to settle on the unoccupied shells, and those which unfailingly became attached to the occupied shells did so also when offered the unoccupied shells. Attempts to relate these individual differences to differences in size or general appearance all failed to reveal any consistent trends.

In Experiment B, with fewer animals and trials, the individual differences are not so marked. However, we see again the same type of distribution, some animals getting on to shells almost every time, some never getting on, with very few showing the random situation, i.e. attaching to the shells in half the trials

Settling of Calliactis *on whelks*

An important feature about the occurrence of *Calliactis* is that it is almost never found on the whelk, *Buccinum undatum*, but exclusively at Plymouth on *Buccinum* shells inhabited by *E. bernhardus*. The experimental animals used in Experiments A and B were used in the same containers to find out whether *Calliactis* would become attached to shells of living *Buccinum*, introduced into the brefitts and plastic bowls, as the hermit-crab shells and crabs had been introduced in the trials described above.

It was found that some of the anemones in the twelve containers of Experiment A did become attached to the shells of the living *Buccinum* almost as quickly as they did to the occupied and unoccupied shells of *E. bernhardus*. However, the whelks usually climbed up the glass and spent much of the time near the top of the container well out of reach of the *Calliactis*, all of which were attached on or near the bottom. Therefore, it is not fair to compare the number of attachments (nine on the single trial performed) with the figures for the hermit-crabs and shells, as a measure of the tendency for *Calliactis* to attach itself to whelks.

Two trials were performed with the animals used in Experiment B with the same experimental arrangements. The five anemones having been allowed to settle on the bowl, the stones, etc., one *Buccinum* was introduced into each of the three bowls. In the first of these trials, seven *Calliactis* out of the total of fifteen, became attached to the three whelks. In the second trial, six became attached. Thus the frequency of settling on whelks was as high as the frequency of settling on the hermit-crab shells in the earlier trials in this experiment. Moreover, when *Eupagurus* were introduced at the end of each of these *Buccinum* trials, the whelks still retained their passenger-anemones, even 24 hours later. It seems, therefore, that the lack of association between *Calliactis* and *Buccinum* in nature cannot be due to any fundamental incompatability of the two species. In these experiments, the anemones lived on *Buccinum* for several days without showing any ill effects or any tendency to desert the whelks. The only obvious difference in the attachment to *Buccinum* was that the shell, being slimy and often covered with a surface deposit, offered an inferior surface for the adhesion of the pedal disc, and the animals were always much less firmly attached for that reason.

The attachment of *C. parasitica* to *Buccinum* is particularly interesting since it shows that the anemone will settle on shells which have had no contact with crabs. The unoccupied shells used in the earlier experiments were almost certainly shells that had once, and perhaps very recently, been occupied by *E. bernhardus*. Therefore, they were not free of all traces of crab occupation as were the shells of living *Buccinum*. This phenomenon particularly underlines the relative unimportance of *E. bernhardus* in the association. It is neither the active initiator of the association nor is it the specific stimulus which elicits the behaviour of *Calliactis* leading to attachment.

Settling of Calliactis *on alkali-cleaned shells*

The stimulus which initiates the sequence of movements by which *Calliactis* climbs on to a shell is undoubtedly one produced by the anemone coming into contact with a shell. Once contact is established, the whole complex manoeuvre unfolds like a pre-arranged programme triggered off by the initial stimulus. Some addititional experiments were done with the animals used in Experiments A and C to find out if chemical stimuli are involved in the process.

Twelve shells which had been thoroughly cleaned by boiling in alkali for several hours were offered to the forty-eight anemones in the twelve containers of Experiment A. Only one of these became attached to a shell during a trial lasting 20 hours, and this was an animal which was not attached to the glass at the beginning of the experiment.

Five of the alkali-cleaned shells were also presented to the twenty *Calliactis* used in Experiment C and in this case too, the result was completely negative ; no *Calliactis* became attached to the shells. This test was repeated several times with the same result. Later on, a number of crabs were induced to enter these cleaned shells and these too were presented to the anemones. The result was again negative ; no *Calliactis* found their way on to the shells. But when five uncleaned shells, occupied or unoccupied, were presented together with the five alkali-cleaned shells, the uncleaned shells acquired their normal

load of two to three *Calliactis* within a few hours, and the cleaned shells remained without passengers.

This preliminary experiment shows that a chemical stimulus contained in the organic deposits which normally exist on a hermit-crab shell is an essential ingredient of the sensory situation which elicits the attachment behaviour of *Calliactis*. Presumably, tactile stimuli arising from the surface properties of the shell are also required. It will be interesting to pursue this matter further and to find out how closely an object must correspond to the surface and shape of a *Buccinum* shell in order to elicit the normal response of *Calliactis* to shells. It should also be possible to narrow down the field of possible chemical stimuli involved in the response. Perhaps here one might obtain a new insight into the powers of sensory discrimination which this anemone possesses. In my experience, *Calliactis* does not move towards shells, occupied or unoccupied, with which it does not come into direct contact. This corresponds with the experience of Davenport (1955) reported in a general review article. He states that in preliminary experiments conducted at Plymouth, adult *Calliactis* showed no ability to " find " shells inhabited by *Eupagurus* and for the association to be effected, immediate propinquity of the two animals was necessary.

DISCUSSION

In these experiments a novel situation in hermit crab/sea anemone associations has appeared, viz., one in which *Calliactis parasitica* establishes the association without the active participation of the crab, *Eupagurus bernhardus*. This situation has a number of interesting implications.

The contrasts between the association here described and the associations between the same species of anemone and the crabs *Pagurus striatus* (Faurot, 1910) and *Pagurus arrosor* (Brunelli, 1913 and Brock, 1927) are striking. With *E. bernhardus*, the anemone climbs on to the shell entirely unaided ; with *P. striatus* it requires preliminary stimulation by the crab to detach its pedal disc, and then it climbs on to the shell as with *E. bernhardus* ; with *P. arrosor*, it requires both preliminary stimulation by the crab to detach its pedal disc and the assistance of the crab in adhering to the shell (described by Brock (1927) as *Auflösen und Aufpflanzen*). Thus we seem to have a series in which the crab assumed an increasingly important, and the anemone a role of diminishing importance, in establishing the association. This is very remarkable. We are familiar with intra-specific differences in feeding habits and in certain types of physiological adaptation in different localities and situations. There are few examples to my knowledge of an ecological association, superficially identical in the end result in all three cases, produced by strikingly different patterns of behaviour, with a shift in emphasis from one partner to the other within the series. Yet these variable features of the relationship suggest that we have here an early plastic stage in the evolution of the habit of association in these pairs of animals.

It cannot be decided, of course, which is the more primitive situation. However, since the *C. parasitica*/*E. bernhardus* association is on the periphery of the range of the anemone, it is a reasonable deduction that it is the most

recently evolved. This would fit the one-sided character of the association with *E. bernhardus*. From this standpoint one might describe the associations with *P. striatus* and *P. arrosor* as two stages in the adaptation of the crab to the presence of anemones on their shells, until the anemones become one of the requirements of normal life for the crab and then it evolved appropriate forms of behaviour to maintain the association. Yet perhaps the behaviour of *Calliactis* in the association with *P. arrosor* should be re-examined before carrying such discussion further since natural interest in the crab's behaviour may have led observers to overlook the less conspicuous activities of the anemone.

We must also revise some of our ideas about the adaptive value of the association in the light of these findings. If *E. bernhardus* is so indifferent to the presence of the anemones as the results suggest, then it is difficult to imagine that the protection which the crab has been believed to obtain from the anemones on its shell, is an important factor in its existence. Certainly the range of *E. bernhardus* extending far up the Irish Sea beyond the range of *Calliactis* (Jackson, 1913) suggests that the survival of this crab owes little to the presence of anemones on its shells.

The active way in which *Calliactis* forms the association points to the conclusion that the association originally had selective advantage for the anemone alone. The habit of attaching to shells could be a development of the habit of attaching to any eminence giving a vantage point for the capture of food. Hermit shells being moved about would have the further advantage of an eminence with some transport provided. The common assumption that *Calliactis* is favourably placed to obtain a portion of the food captured or gathered by the hermit crab is not well substantiated. Indeed, their position on the shell, usually behind and far above the crab and its feeding appendages, makes it difficult to see how the anemones can get much food in that way. The activity described by Orton (1922) whereby *Calliactis* "sweeps" the bottom with its tentacles to obtain particles scattered by the crab hardly seems likely to yield the quantities of food which would justify the evolution of this complex behaviour pattern.

Certain general adaptations of *Calliactis parasitica* to shells of *Buccinum* occupied by *E. bernhardus* have not received much comment in standard descriptions, e.g. Stephenson, 1935. So closely do the lines and markings and general coloration of the anemone correspond to the grooves and ridges and blotchy colouring on the shell that it is often very difficult to make out the exact boundary of the pedal disc on the shell. Colour photographs show this very clearly and it is apparent even in the eight black and white photographs shown in the two plates.

Perhaps the most interesting element in the association of *C. parasitica* with *E. bernhardus* is the demonstration of a highly co-ordinated programmed activity definitely related to a highly specific goal. Pantin has drawn attention several times (1950, 1952) to other activities of sea anemones which are directed towards a goal. Thus the "searching" behaviour of *Metridium* when food is placed nearby, after making allowances for the extraordinarily slow time scale, has many of the features associated with activities involving

central nervous co-ordination in other animals. The behaviour of *Calliactis* when it makes contact with a shell seems to be perhaps the most remarkable of such activities. The subsequent movements show a co-ordination which must be based on the accurate flow and scanning of information about the chemical and physical properties of the shell surface and its position with respect to gravity, together with information fed back as the sequence of movements unfolds. This whole sensory input is directed into motor channels which lead to activities, some of them asymmetrical, which follow each other in an orderly sequence. We are in no position yet to attempt an analysis of this remarkable activity in terms of a co-ordinating sensory-motor complex. Yet if the lives of these animals are ever to be understood in any real sense, the structural and functional basis of this slow but unerring co-ordination will have to be discovered.

SUMMARY

1. Observations and experiments on the association between *Calliactis parasitica* and *Eupagurus bernhardus* have been carried out.

2. The attachment of the anemone to the shell is achieved by a remarkable manoeuvre involving the attachment of the tentacles and oral disc, the freeing of the pedal disc and its adhesion to the shell by a somersaulting movement, with the eventual release of the oral attachment and the assumption of the normal posture on the shell.

3. Active participation of *E. bernhardus* in detaching the anemone and transplanting it on the shell was not observed, in contrast to the active parts played by the crabs *Pagurus striatus* and *P. arrosor* in their associations with *C. parasitica*.

4. *C. parasitica* becomes attached to empty shells no less quickly or frequently than to shells occupied by *E. bernhardus*.

5. The anemone readily settles on shells of living *Buccinum undatum* in the laboratory and does not desert these for shells occupied by crabs. It does not settle on shells cleaned by boiling in strong alkali.

6. The respective roles of anemone and crab in the associations between *Calliactis* and these three species of pagurid crabs are discussed from the standpoints of comparative behaviour and with special reference to the capacities of the actinian neuromuscular system here displayed.

ACKNOWLEDGMENTS

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EXPLANATION OF THE PLATES

Plates 1 and 2

Eight stages from a series of twenty-nine photographs showing the attachment and settling of *Calliactis parasitica* on a shell occupied by *Eupagurus bernhardus*.

(a) Establishment of contact between anemone attached to wall of tank and shell (small area of pedal disc not securely attached). (b) Tentacles exploring shell and adhering to it. (c) Tentacles establishing firm attachment to shell ; column of anemone twisting ; pedal disc loosening its hold on glass. (d) Oral disc expanded to provide large area adhering to shell ; pedal disc freely suspended ; column bending to bring pedal disc into position for attachment to shell. (e) Portion of pedal disc in contact with shell, becoming swollen and turned up at the edge ; oral disc and tentacles still firmly adhesive. (f) Area of attachment of pedal disc spreading out to periphery by general swelling with local puckering at the edge ; oral disc beginning to free itself. (g) Most of pedal disc now attached, assisted by a constriction of the column immediately above it ; oral disc detached and column beginning to straighten out. (h) Anemone in final position on shell, having climbed slightly higher than in (g) ; pedal disc firmly attached, column upright and oral disc expanded.

Approximate times involved beginning from (a) : (b)—2 min.; (c)—5 min.; (d)—9 min. ; (e)—14 min.; (f)—18 min. ; (g)—22 min. ; (h)—35 min.

Crab moved between (a) and (b) ; crab moved and camera was moved between (d) and (e) ; crab moved between (e) and (f).

TAXONOMIC NOTES ADDED IN PROOF

1. By Opinion 472 of the International Committee on Zoological Nomenclature, the generic name *Eupagurus* is now suppressed in favour of *Pagurus*.

2. The specific names *arrosor* (Herbst) and *striatus* (Latreille) are apparently synonyms (Bouvier, 1940). Remarks on these in the text refer in fact to *P. arrosor* (Herbst) from Naples and Banyuls respectively.

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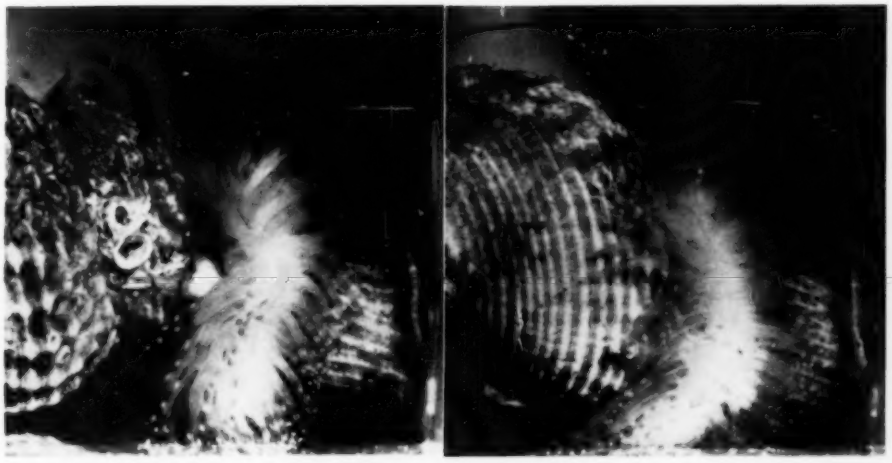
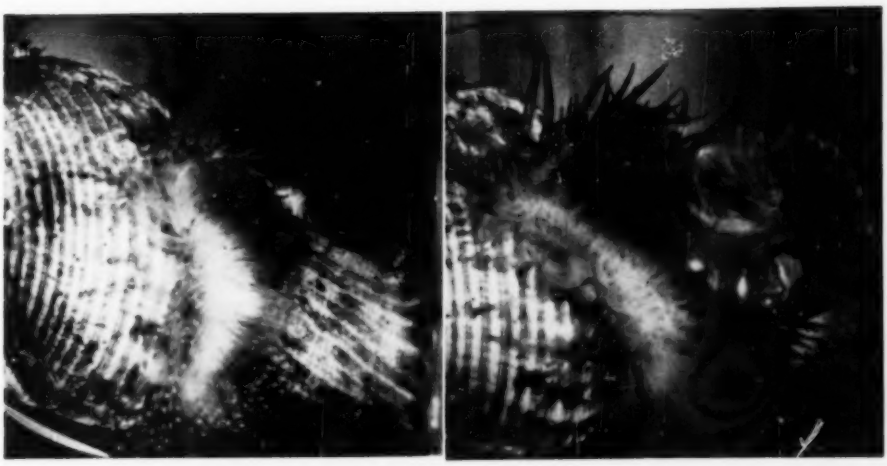


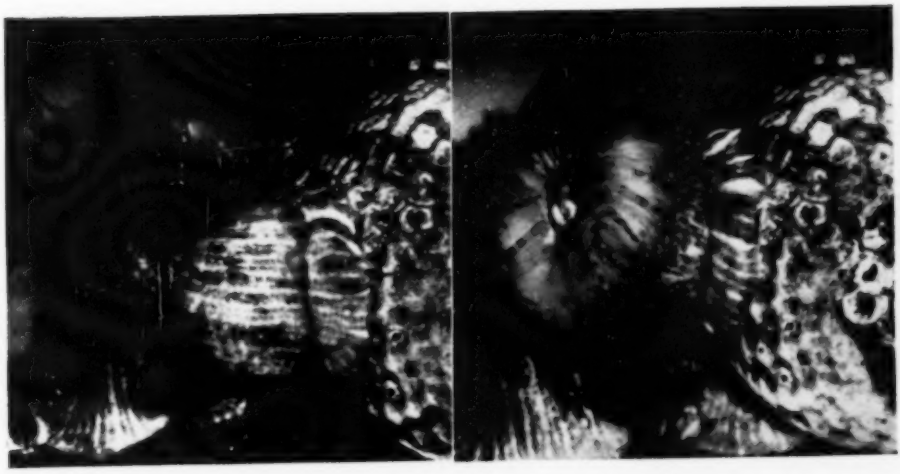
a b



c d

The attachment and settling of the sea anemone *Calliactis parasitica* on a shell occupied by the hermit crab *Eupagurus bernhardus*.

e f



g h

The attachment and settling of the sea anemone *Calliactis parasitica* on a shell occupied by the hermit crab *Eupagurus bernhardus*.

e f

g h

The attachment and settling of the sea anemone *Calliactis parasitica* on a shell occupied by the hermit crab *Eupagurus bernhardus*.

THE AFRICAN STRIPED WEASEL, *POECILOGALE ALBINUCHA* (GRAY)

BY

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[Accepted 14th April 1959]

(With 1 plate)

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INTRODUCTION

Poecilogale albinucha has a wide range in central and southern Africa, but is rarely seen or collected, and practically unknown in captivity. It is therefore not surprising that much of its life history remains obscure. In this paper some observations on a tame female formerly in my possession are given and published data is correlated.

" White-naped Weasel " is simply a transliteration of *albinucha*, and not used in practice. In fact the animal is so little known generally that it can hardly be said to have a common name at all. " African Striped Weasel " has, however, been used by Shortridge (1934) and subsequently by the magazine "African Wild Life," and seems suitable in every way.

My tame striped weasel, " Susie " (see Plate 1) was completely amenable to handling. Caught at Kasama, N. Rhodesia, in March 1957, she later came into my possession, and was kept at Ndola until November when I took her to the U.K. She was presented to the Zoological Society of London in January 1958, being the first live one received at Regent's Park during this century. The only others on record there were two in 1897, which are presumably those described by Pocock in his paper of 1927. Unfortunately Susie did not survive long, and died in February, the immediate cause being enteritis,

which itself was due to fairly long-standing tuberculosis of the spleen (L. Harrison Matthews, *in litt.*). Possibly she might have lived longer if remaining in Africa, though Haagner (1920) records that the species does not thrive in captivity, which seems to accord with Hoier's experience in the Belgian Congo (Hoier, 1955).

DISTRIBUTION

The general distribution of the species is given by Ellerman *et al.* (1953), but its precise limits remain obscure in many places, due to the infrequency with which it is collected.

TAXONOMY

In addition to the nominate race several subspecies have been described, but most appear little substantiated, and founded on the basis of few specimens only. To assess their true status comparison of material from all over the species range would be required, and until this can be done it is not possible to say which may be valid and which not.

VARIATION IN DORSAL STRIPING

The dorsal pattern consists of four light and three black stripes, and museum skins often vary in the colour of the light ones, from whitish to fairly deep orange buff. Hill & Carter (1941) remark on this as follows. "The dorsal stripes frequently are near Deep Colonial Buff or even near Honey Yellow. However, these have the appearance of discoloration and in animals from the same locality the stripes may be nearly pure white, so that no systematic value can be attached to these variations."

These authors appear to be mistaken in regarding the yellowish striped skins as necessarily discoloured, for while post mortem colour change may indeed take place, my experience from living and freshly killed animals, as well as native-made specimens in various states of preservation, is that the normal colour of the stripes in life is some shade of yellow or buff, and the whitish ones are unusual.

I have seen only one skin in Northern Rhodesia with whitish stripes, and this seemed probably bleached by long exposure to light. At the other extreme I obtained two skins with deep orange stripes, which looked quite obviously discoloured. I washed them in soap and water, and the result was two perfectly normal, i.e. light yellow striped, skins. In this case I think wood smoke in the hut where they had been kept was responsible.

The issue is, however, complicated by the fact that the colour of the stripes may alter in the living animal. I have observed this in my own specimen, in which they varied from light yellow to quite deep buff, this latter not very different from the discoloured skins mentioned above. I am unable to say whether such variation is correlated with age, season, or any other factor, but it does occur. The tail, head and neck are always white or off-white, though there may be a yellowish suffusion on the edges of the central black stripe where it enters the white of the neck.

One further point in connection with the dorsal stripes is that there is often along the central (black) stripe, in its hinder part, a narrow margin of pure white on each side, separating the black and yellow. This is in contrast to both other colours and proves beyond doubt that the yellow is not necessarily due to staining, for if it were the white would not show in this way.

It follows, therefore, as Hill & Carter have said, that colour as a racial character must be used with caution, but it is the white rather than the yellow stripes which are less frequent. Races which have been named on colour differences in only one or two specimens may well prove invalid when longer series are examined.

THE SCENT GLANDS

On either side of the anus are more or less oval shaped scent glands, which can be distinctly felt in the living animal. These secrete a noxious fluid, which is discharged under the influence of alarm. Pocock (1927) was incorrect in supposing this might not be so, but the habit is rightly noted by Roberts (1951).

The smell thus generated, though strong, is not excessively so, nor especially persistent. The coloration of the animal, however, must undoubtedly be of true warning significance.

FOOD

The striped weasel is carnivorous, and little probably comes amiss to it in the way of small mammals and birds, which it may, according to Shortridge (1934) and Theiler (1951), kill up to the size of the springhaas (*Pedetes*) and guinea fowl (*Numida*). These authors also list lizards, locusts and eggs among its diet, and it has apparently been known to take poultry at times. Cowles (1936) cites a native report of a striped weasel killing a mamba (*Dendroaspis*). Cunnison (1951) states that according to local African information in N. Rhodesia " moles " (i.e. *Cryptomys*) form a large part of its prey. I have heard this too, and Verheyen (1951), also quoting native information, says the same, and further gives an account of how they are alleged to catch them. Apropos of this it may be noted that one of the most common African methods of catching *Cryptomys hottentotus* is to open up a burrow, and then wait till the animal comes out, when it is caught by cutting off its retreat with a stick thrust into the hole behind it at a point where the earth has previously been pared down with a hoe until the remaining roof of the tunnel is very thin, offering no resistance to the stick. I have always supposed it was the draught of cold air blowing in the tunnel that told the mole rat its hole was open, upon which it would come to close it. How much the scent of the striped weasel would be instrumental in bringing it out is doubtful, and I think this part of Verheyen's account must be taken with reserve. The method of killing guinea fowl, outlined by Cunnison (op. cit.), appears fanciful. It seems probably no more than fable and I would be inclined to doubt it as given. I have seen ' Susie ' climb into low scrubby trees which do not present a large area of bare upright trunk, but I think the animal would probably be disinclined to climb much in the wild state.

Roberts (op. cit.) suggests that its claws are more suited to holding prey than those of *Ictonyx*, but, while they are indeed shorter, my observations of 'Susie' lead me to suppose that in fact it does not use its paws for holding prey either during capture or when feeding.

VOICE

The animal is normally completely silent. Only once did I ever hear 'Susie' make any sound, and this was when greatly upset. I offered her a freshly killed bird to which, for some unknown reason, she took the greatest exception, and let out a noise, difficult to describe exactly, but harsh and loud, and somewhere between a growl and a scream.

SENSES

Both Shortridge and Theiler (op. cit.) state the striped weasel hunts mainly by scent, and there is no reason to doubt this. When running on the ground it sniffs audibly and more or less continually. 'Susie' would hunt me by scent but appeared to do so less easily than a dog. She used her eyes a good deal more than I would have thought likely in an animal so low to the ground, with a presumably restricted field of vision. She would chase me by sight at full speed and could certainly see me well enough at several yards distance. It is, of course, not always easy to judge from a tame animal what its behaviour would be in the wild state, but it seems fair to say that the sense of smell in the species is good, though not excessively so, and the eyesight keen. Hearing appears good, though not especially sharp.

TAIL CARRIAGE

Normally the tail is carried more or less in line with the back, or drooping slightly towards the ground. When encountering an interesting scent it is raised vertically. Under stress of alarm it is fluffed out like that of a mongoose in similar circumstances, no doubt part of the "warning" technique.

GENERAL HABITS

Roberts (op. cit.) noted that it was usually in threes and was largely (he thought perhaps wholly) diurnal. Two specimens, male and female, killed at Kasempa were abroad at about 7 a.m. On the other hand Shortridge (op. cit.) considered it mainly nocturnal, while Hoier (op. cit.) and Curry-Lindahl (1956) record seeing the species by night. Handley (1951), though assuming it to be mainly nocturnal, nevertheless reports seeing one by day himself, and hearing of two others killed in daylight. From these data it seems clear that the animal is neither exclusively diurnal nor nocturnal. The normal association seems pairs, threes, or family parties. It is undoubtedly mainly terrestrial though able to climb reasonably well. The shape of its body unmistakably indicates fossorial habits. Susie would "go to ground" whenever possible, and because of the remarkable suppleness of the body, clearly shown in the Plate, could turn round completely in a very narrow space.

BREEDING

Little is recorded of the breeding habits of the species. 'Susie', when caught, was about half grown, in March. Shortridge (op. cit.) mentions two foetuses from Sesheke district in October.

MAMMARY FORMULA

While most of the external characters have been well described by Pocock (1927) no mention is made of mammary formula. Neither have I seen any record of this elsewhere, but in an adult female from Kasempa, N.R. there were three pairs of nipples in the lower abdominal region, while another, also from Kasempa, had only two pairs. In each case the rearmost pair was noticeably larger than the others.

NUMBERS

While the striped weasel is very seldom seen, it may, nevertheless, not be quite as rare as generally supposed, though by comparison with such abundant species as the genets, and several other lesser carnivores, it is undoubtedly uncommon. A fair number of skins can be found in villages and the animal is quite well known to rural Africans. Cowles and Cunnison (op. cit.) both mention its use in native medicine.

SUMMARY

An account is given of what is known of the habits and life history of *Poecilogale albinucha* drawn from published records supplemented by observations of a tame female formerly in the writer's possession.

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ADDENDUM

It is surprising that two separate accounts of the captivity behaviour of an animal so seldom kept alive should be written almost simultaneously, but since the above went to press an article on a pair of semi-captive *P. albinucha* in South Africa has appeared (Alexander & Ewer, 1959).

It is therein confirmed that the fore paws are not used in capturing prey, or in holding it when feeding, and the habit of hiding away surplus food is noted. My own striped weasel would kill as many mice as she was offered, and would likewise hide them in her sleeping box. She failed to kill a really large female *Mastomys natalensis*, though a fully adult animal might have done so, and a pair would probably have had no difficulty at all.

Alexander & Ewer found their striped weasels indifferent to certain birds, but mine, as noted in the text above, reacted violently the only time I offered her a bird (a small passerine). The voice when angry is described by these authors as " half growl, half shriek " which confirms my own description.

I do not agree with Alexander & Ewer that its alleged poultry raiding propensities are likely to cause reduction in its numbers. While very uncommon indeed in captivity, seldom observed wild, and scarce in museum collections, I consider it may not be quite as rare as often supposed, and while plenty of suitable habitat remains (as seems likely for the foreseeable future) it is improbable that human predation, which is infrequent, will affect its status.

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African Striped Weasel, *Poecilogale albinucha* (Gray).

THE BRITISH SPECIES OF *BUGULA* (POLYZOA)

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(With 3 plates and 15 figures in the text)

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INTRODUCTION

This paper describes the appearance and characters of eleven species of *Bugula* known to occur in British waters. The most useful existing account of this genus is that given in the British Marine Polyzoa (Hincks, 1880), but only six of the species described below are included in that work. These are *Bugula avicularia* (L.), *B. turbinata* Alder, *B. flabellata* (Thompson), *B. calathus* Norman, *B. plumosa* (Pallas) and *B. purpurotincta* Norman. *B. neritina* (L.), a cosmopolitan species, is established in a number of localities on southern coasts of the British Isles. Probably first introduced fifty or sixty years ago, there is still no readily available description in English, and no account of its distribution in Britain. *B. simplex* Hincks, another widely distributed species, has only recently been recognized in this country (Ryland, 1958 a), although

it has apparently been present for many years. Three other species, which do not appear to have been previously described, occur at least in the southern half of the British Isles. Again the evidence shows that they have been present for many years. In addition to the six previously referred to, Hincks (1880) describes two other species of *Bugula*. The species called *B. murrayana* is now placed in the genus *Dendrobeania* (Levinsen, 1909). The other, *B. gracilis* var. *uncinata* Hincks, is in fact quite clearly not a variety of *B. gracilis* at all. It is almost certainly *B. turrita* (Desor), a well-known American species. It seems very probable that Hincks was in error in thinking his specimen to be of British origin; however a short description of *B. turrita* is given on p. 98 of this paper. Calvet (1900) gives a useful account of some of the species found on the south coast of France. These are *B. simplex*, *B. calathus*, *B. turbinata*, *B. avicularia* and *B. neritina*, all of which are described below.

While the account of the British species was in preparation, it became apparent that considerable confusion surrounded the identity of a number of species of *Bugula*. While a complete revision of the genus is beyond the scope of the present paper, it seemed important to make quite clear the distinctions between those British species and superficially similar ones with which, outside the British Isles, they were being confounded. Full synonomies have been included only for those species involved in some sort of taxonomic confusion.

Types and figured specimens have been deposited at the British Museum (Natural History). In the following account specimens in the British Museum collections are indicated by a registered number preceded by the abbreviation B.M.N.H.

GENERAL ACCOUNT OF THE GENUS *BUGULA*

Definition of the genus

Family : Bugulidae Gray, 1848.
Genus : *Bugula* Oken, 1815.
Genotype : *B. neritina* (L.), see Harmer (1923, p. 299).

Zoarium erect and branching ; unilaminar. Zooecia arranged in two or more series, alternate ; boat-shaped, with the proximal end forked : the distal end of the next lowest zooecium wedged into the fork, but extending beyond it on the frontal side. Seen frontally the zooecia are usually truncate above and slightly attenuated towards the base. The basal and lateral walls are calcified, but the frontal surface is mainly or wholly occupied by the opesia and the gymnocyst is correspondingly short. The opesia is covered by the frontal membrane, from which the operculum is not clearly differentiated. One or more spines may be present, especially on the distal angles of the zooecium. An avicularium shaped like a bird's head is present on the lateral margin or on the frontal surface of all or many of the zooecia ; in rare cases avicularia are wanting. Ovicells hyperstomial, typically globular but sometimes reduced in size, on the distal margin of the zooecium.

Harmer (1926) and Hastings (1943) maintain a single family, Bicellariellidae (Levinsen, 1909), which includes *Bugula*, *Bicellariella*, *Beania*, and related genera. Instead of this comprehensive family, Bassler (1953) recognizes three families : Bugulidae, Bicellariellidae and Beaniidae. He points out that the name Bugulidae has priority over Bicellariellidae so that, irrespective of the view taken as to the compass of the family, the correct placing of *Bugula* is in the Bugulidae.

Some of the British species may be found on the shore, and *B. turbinata* is often plentiful in gullies and under boulders near low water mark. In general, however, the British species are characteristic of shallow water. Pier piles, floating pontoons and other permanently submerged structures often carry a fauna in which a number of species of *Bugula* are conspicuous. Six species, four of them not included in Hincks' (1880) account, have been found on test surfaces being used for fouling studies, and the species settling have often been abundant, forming a conspicuous part of the fauna on the panels (Pl. 3 A). To facilitate the identification of young colonies the ancestrulae have been described whenever possible.

Characters of systematic value

The most useful characters for the separation of species are discussed below.

(i) *Size and form of the zoarium.*

Many species, particularly those with zooecia in two series, have branches disposed spirally around a central axis (Pls. 1 A, 2 E, F). In others the zoarium is tufted (Pls. 1 C, D) or, in multiserial species, cup or saucer shaped. The height of the colony is also important as quite large differences are found between species.

(ii) *Number of series of zooecia.*

A general distinction may be made between biserial and multiserial species. Some seem invariably biserial, others show a tendency to become tri- or quadriserial a short distance below bifurcations in the distal part of the colony. In genuinely multiserial forms six to nine rows of zooecia are present and consequently the branches are very wide.

(iii) *Bifurcations.*

In strictly biserial species the arrangement of zooecia at a bifurcation conforms to one of three patterns (Fig. 1). This character was first recognized by Harmer (1923, 1926), and in his terminology the bifurcations are described as types 3, 4 or 5. Ignoring the most proximal bifurcations, the type is usually constant in any colony and throughout the species, although exceptions do occur. The bifurcations are best observed from the basal side in stained and cleared specimens. The pattern of consecutive bifurcations is laterally reversed, so that the bifurcations immediately above and below any given one are mirror images of it. The arrangement of zooecia is denoted by letters. The first zooecium from which two zooecia are budded in preparation for the bifurcation is referred to as A, the one beside it as B (Fig. 1). The outer zooecia above A and B are C and D respectively, while the inner zooecia are E and F.

In bifurcations of type 3 the inner angle is formed by zooecia E and F (Fig. 1A). In type 4 the inner angle is formed by F and G—G being immediately distal to E in the same series. Zooecium E has become completely enclosed, and the

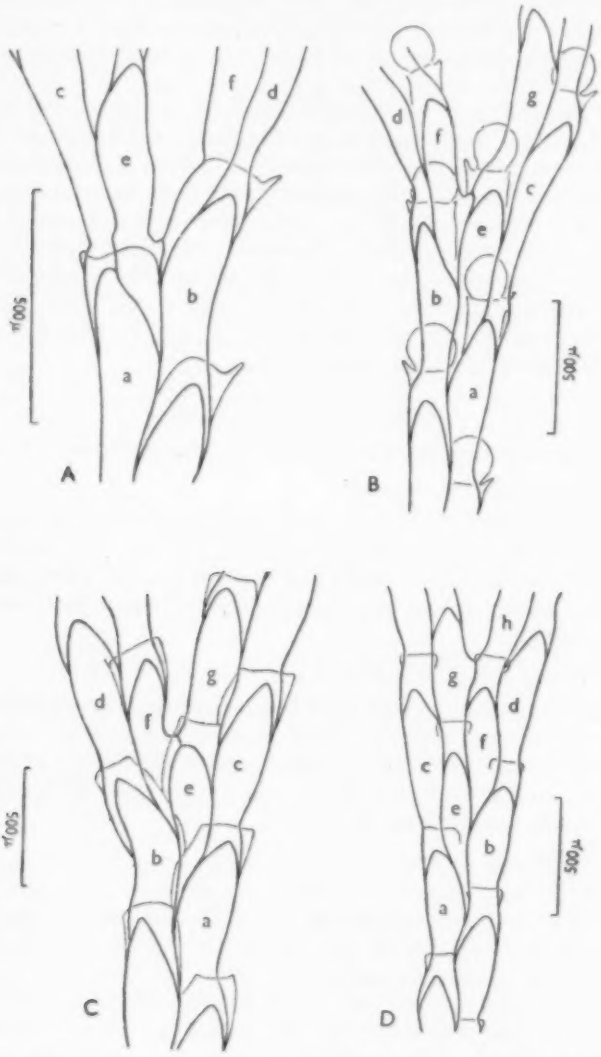

Fig. 1.—Types of bifurcation found in *Bugula* seen from the basal side (for full explanation see text). A. Type 3 (*B. plumosa*, Harwich). B. Type 4 (*B. stolonifera* : holotype). C. Type 4 (*B. neritina*, Swansea Docks ; B.M.N.H. 1959.3.18.16). D. Type 5 (*B. fulva:* holotype). In the case of *B. fulva* bifurcation tends to be achieved by bisection of a branch which has become quadriserial. Zooecium H does not show the narrow connexion with G as in the examples given by Harmer (1923, 1926).

TABLE I

Zooecial dimensions of some species of *Bugula*. Each entry is based on the measurement of 20 zooecia (15 in *B. purpurotincta* and *B. aquilirostris*) accurate to the nearest 5μ. For explanation and discussion see text (p. 70)

Species	Locality	Zooecial length		Zooecial width		Length/Width	
		Mean (μ)	Standard deviation (μ)	Mean (μ)	Standard deviation (μ)	Mean	Standard deviation
B. neritina	Swansea	745	103	255	32·5	2·95	0·21
B. plumosa	Harwich	495	39	150	10·0	3·34	0·31
B. turrita	Woods Hole (U.S.A.)	490	38	140	11·5	3·70	0·32
B. purpurotincta	Shetland	560	40	165	12·5	3·47	0·33
B. stolonifera	Swansea	700	75	165	13·0	4·25	0·55
B. stolonifera	Milford docks	740	43	180	15·0	4·20	0·42
B. avicularia	Norfolk	605	37	180	17·5	3·36	0·31
B. turbinata	Milford Haven	550	39	180	17·0	3·22	0·39
B. flabellata	North Sea	800	66	170	32·0	4·38	0·84
B. fulva	Menai Straits	625	24	160	13·5	3·97	0·44
B. fulva	Harwich	650	61	165	14·0	3·95	0·50
B. fulva	Naples	540	48	155	13·0	3·45	0·38
B. calathus	Bardsey Island	650	37	170	13·5	3·85	0·39
B. aquilirostris	Bournemouth	600	56	210	21·0	2·91	0·94
B. simplex	Holyhead	750	82	140	15·0	5·40	0·95

proximal part of G connects with zooecium F (Figs. 1B, C). In type 5 the enclosing process has been further extended so that both E and F are completely surrounded. The inner angle is, therefore, formed by zooecia G and H (Fig. 1D). It should be noted, however, that the connecting portion between G and H may be very slender.

(iv) *Zooecia.*

The most important characters are the shape and size of the zooecium, and the relative lengths of the opesia and gymnocyst. The latter character can easily be seen and described, and features in the majority of descriptions. Measurements must be made accurately and it is essential to use cleared and mounted specimens. The characters that seem most useful are the mean length, and the length/width ratio ; but until many measurements have been made on material from different localities, it will not be possible to assess the amount of variation and, consequently, the full taxonomic value of such data. Measurements made on the species discussed in this paper are given in Table 1. These have all been made from the basal side and measure the distance between two zooecial apices, and the maximum width. It is most important that any zooecium at the proximal end of a new series should not be included : in biserial species these are zooecia C, D, E and F at a bifurcation (Fig. 1), but in multiserial forms they may occur anywhere. Inclusion of these will seriously affect both the mean and the standard deviation of the resulting data and make valid comparisons impossible. In the multiserial species measurements were made only of zooecia in the inner series, and bifurcations avoided. Measurements should be spread between the proximal and distal parts of the zoarium to cover any possible positional variation.

(v) *Spines.*

The number of spines developed on the upper distal angles of the zooecia forms one of the most useful criteria for classifying members of the genus. The outer angles usually have a greater number of spines than the inner ; otherwise the armament is very constant. The number of spines present is most easily given as a formula, the outer angle being written first. Thus 3 : 2 indicates three spines on the outer distal angle and two on the inner.

(vi) *Ovicells.*

A well-formed ovicell (ooecium) occurs in all the British species, but the shape varies from hemispherical (Figs. 5 and 13) to globular (e.g. Fig. 4).

(vii) *Avicularia.*

(a) *Presence or absence of avicularia.* Avicularia are present in all the British species except *B. neritina.*

(b) *Position of attachment.* In the British species a zooecium of the marginal series is provided with an avicularium attached to its outer margin. It may be situated just below the distal spines or some way down the opesia, but the position is constant in any species. In multiserial species the inner series of zooecia may, or may not, bear avicularia ; when present they are smaller than those found on the marginal series.

(c) *Size.* The most useful expression of size is obtained by comparing the length of the avicularium with the width of the zooecium bearing it. Thus

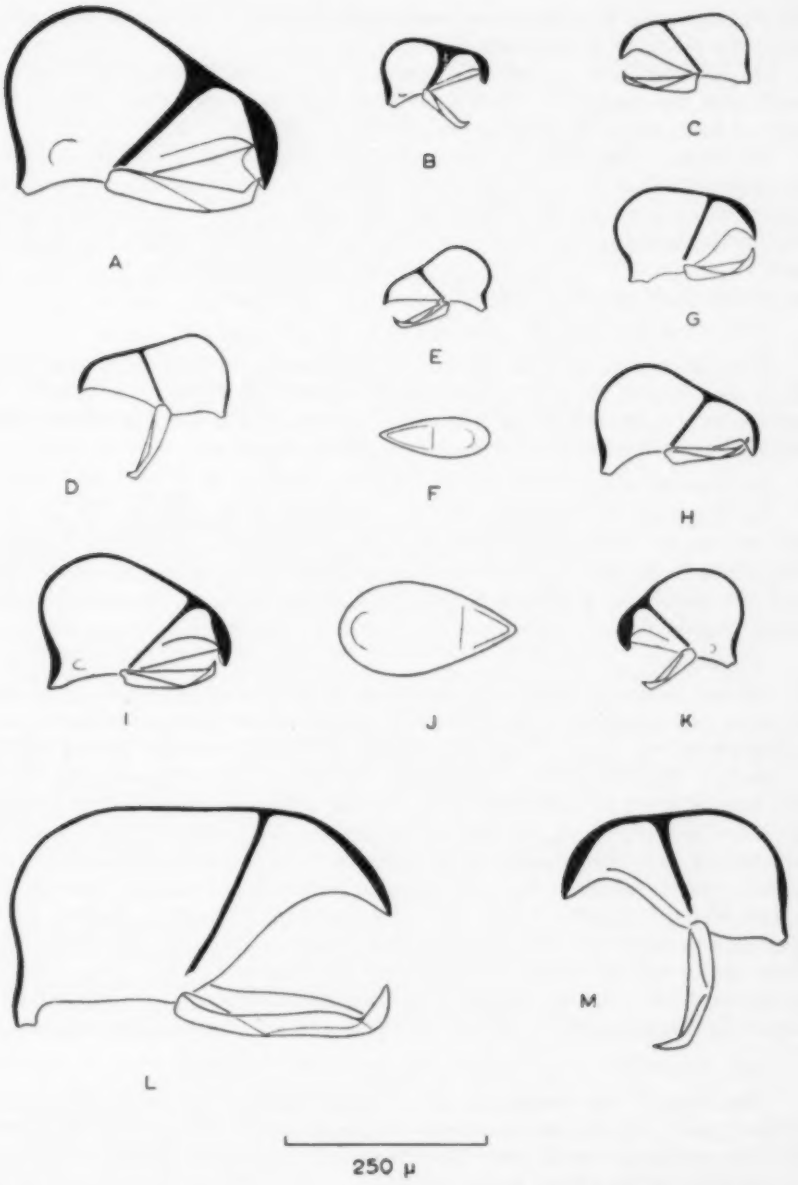

Fig. 2.—Avicularia of the British species of *Bugula*. A. *B. flabellata* ; from a marginal zooecium, profile. B. *B. flabellata* ; from an inner zooecium, profile. C. *B. simplex* ; profile. D. *B. purpurotincta* ; profile. E. *B. plumosa* ; profile. F. *B. plumosa* ; seen from above : avicularia of the other species, except *B. turbinata*, are similarly proportioned. G. *B. stolonifera* ; profile. H. *B. fulva* ; profile. I. *B. turbinata* ; from a marginal zooecium, profile. J. *B. turbinata* ; seen from above to show the inflated head. K. *B. turbinata* ; from an inner zooecium, profile. L. *B. calathus* ; from a marginal zooecium, profile. M. *B. avicularia* ; profile.

the length varies from less than the zooecial width in *B. plumosa* to about twice the width in *B. calathus*.

(d) *Ratio of beak to head.* The parts of an avicularium are the head, the beak, and the mandible which articulates with the base of the beak. The ratio of beak length to head length provides a useful character.

(e) *Shape.* The shape of the avicularium, especially in profile, is highly characteristic (Fig. 2). The drawings convey the appearance more accurately than written descriptions. However, the shape of the beak is such a useful diagnostic character that the terms " abruptly hooked " (Figs. 2A, B, I, K) and " downcurved " (Figs. 2C, G, H, L, M) are used in the key to species and in the descriptions which follow.

(viii) *Tentacle number.*

With the exception of *B. neritina*, the number of tentacles is usually about 13 or 14. Slight variation occurs, and occasional polypides are found with one tentacle more or less than the usual number, which seems, however, sufficiently constant to provide a useful secondary character.

(ix) *Embryo colour.*

In all the species observed, with the exception of *B. neritina*, the colour of the embryo was some shade of yellow (Ryland, 1958 b). While this character provides a further distinction from other cellularine genera such as *Bicellariella* and *Scrupocellaria*, it affords no help in the separation of species within the genus *Bugula*.

(x) *Larvae.*

All the cellularine Polyzoa have larvae of a very similar type. They are more or less spherical or, more usually, plum shaped and generally of a pale yellowish-brown colour. Apically, surrounded by a ciliary corona, is the " calotte " (Barrois, 1877). Below this the rest of the surface is covered by the vertical rows of locomotor cilia. In the larvae of many species pigment spots are present, whose number and disposition, although subject to a certain amount of variation, should not be overlooked as a taxonomic character (see p. 93). On the anterior face, and running vertically, is a median groove, just above which is a tuft of long cilia, the " plumet vibratile " (Calvet, 1900). This groove, together with the associated glandular structures, forms the pyriform organ which assists in temporary attachment of the larva prior to metamorphosis. Larval morphology and metamorphosis are described in detail by Barrois (1877), Calvet (1900), Grave (1930) and Lynch (1947).

(xi) *Ancestrula.*

The form of the ancestrula, the number of spines placed on the margin of the opesia, and the number, shape, and degree of development of the primary stolons constitute useful characters, especially in fouling studies where very young colonies may have to be identified.

KEY TO THE BRITISH SPECIES OF *BUGULA*

1. Avicularia present ..... 2.
   Avicularia absent. (Zoarium purplish-brown when living, trans-

lucent brown when dead; zooecia large (Table 1); ovicells attached to the inner distal angle of the zooecia, orientated obliquely to the axis of the branch) ..... *neritina* (p. 74).

2. Inner distal angle of zooecium unarmed, outer angle with one projection or spine; bifurcations of type 3 (Fig. 1 A) ..... 3.

Both distal angles bearing at least one spine; at least the majority of bifurcations not of type 3 (Figs. 1 B, C, D) ..... 4.

3. Ovicell globular; avicularia very small, their length less than the width of a zooecium; outer distal angle drawn out into a pointed projection ..... *plumosa* (p. 76).

Ovicell hemispherical; avicularia larger, their length equalling the width of a zooecium; outer distal angle bearing a jointed spine *purpurotincta* (p. 76).

4. Outer distal angle of zooecia bearing one or two spines, inner bearing one spine ..... 5.

Both distal angles bearing at least two spines ..... 9.

5. Zooecia biserial ..... 6.

Zooecia multiserial ..... 8.

6. Outer distal angle bearing two spines; beak of avicularium downcurved (Figs. 2 G, M) ..... 7.

Outer distal angle bearing one spine; beak of avicularium very short, abruptly hooked (Fig. 2 I). (Branches may be multiserial distally) ..... *turbinata* (p. 81).

7. Zoarium tufted, the branches not spirally arranged (Pl. 1 C); zooecia long and slender, the opesia occupying two-thirds to three-quarters of the total length; avicularia fairly small (about 175 μ long) their length not exceeding the width of a zooecium (Fig. 2 G) *stolonifera* (p. 79).

Zoarium with branches spirally arranged (Pl. 1 A); opesia occupying almost the whole of the frontal surface; avicularia large (about 300 μ long) their length exceeding the width of a zooecium (Fig. 2 M) ..... *avicularia* (p. 80).

8. Ovicells hemispherical; avicularia restricted to the marginal series of zooecia, beak downcurved (Fig. 2 C) ..... *simplex* (p. 91).

Ovicells globular; large avicularia present on the marginal zooecia, small ones on the inner series, the beak always abruptly hooked (Figs. 2 I, K) ..... *turbinata* (p. 81).

9. Beak of avicularium abruptly hooked (Fig. 2 A) ..... *flabellata* (p. 82).

Beak of avicularium downcurved (Figs. 2 H, L, 12 B) ..... 10.

10. Zoarium biserial (sometimes quadriserial before distal bifurcations in well-grown colonies); spine formula 3 : 2, the spines well-developed but fairly small ..... *fulva* (p. 86).

Zoarium bi- or quadriserial, sometimes more; spine formula 3 : 3 (2 : 2 in presence of ovicell), the uppermost spine on the outer angle usually longer than any of the others; avicularia present on all, or almost all, zooecia, those on the marginal series being larger—but not more than about 250 μ in length—and somewhat exceeding the width of one zooecium ..... *aquilirostris* (p. 89).

Zoarium multiserial; spine formula 2 : 2 on the inner zooecia, 3 : 2 or 2 : 2 on the marginal ones; avicularia on the marginal zooecia very large, about 400 μ long, their length equalling or exceeding the width of two zooecia; small avicularia may be present on a few of the inner zooecia ..... *calathus* (p. 87).

SYSTEMATIC ACCOUNT OF SPECIES

B. NERITINA (Linnaeus)

Figs. 1 C (bifurcation), 3 A, B ; Pl. 2 C

Description

Living zoarium of a purplish-brown colour forming luxuriant tufts of up to 8 cm. or more in height. Fixed material is a distinctive translucent brown. The tips of the branches show slight spiral growth, but the colony as a whole

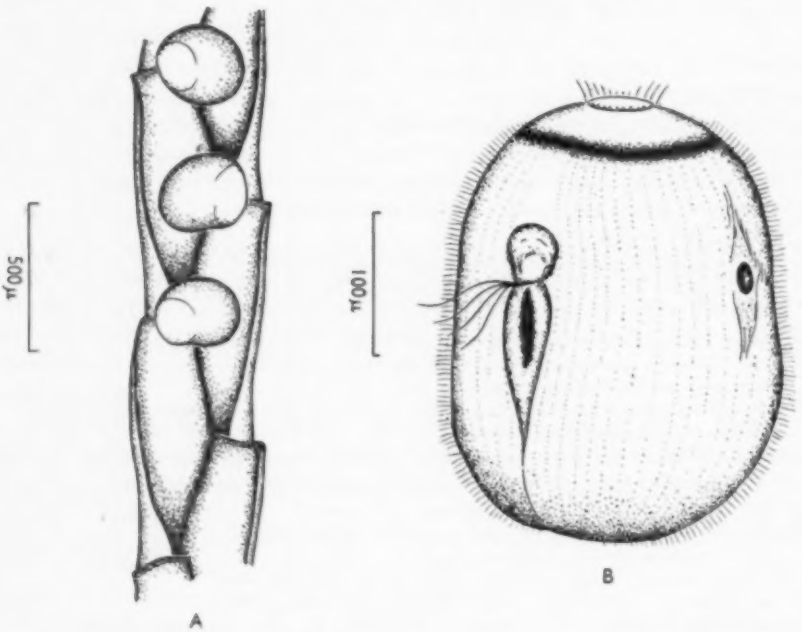

Fig. 3.—*B. neritina*. A. Portion of branch bearing ovicells seen in frontal view ; Swansea Docks. B. Larva.

is not spiral. The branches are biserial, with bifurcations of types 4 or 5. Zooecia large, narrowing below, the opesia occupying the whole of the frontal surface. Spines absent, although the free upper angle of the outer margin may form a slight projection. Avicularia absent. Ovicells attached to the inner distal angles of the zooecia, orientated obliquely to the axis of the branch ; aperture concealed. Polypide with 23 or 24 tentacles (Calvet, 1900 ; Hastings, *in litt.*).

Habitat

Calvet (1902 a) records *B. neritina* as occurring in the littoral zone, but in Britain it is a shallow water form growing luxuriantly on pier piles and similar structures. It settles readily on immersed test surfaces.

Breeding

At Swansea, in a dock artificially warmed by a power-house effluent (Naylor, 1959 ; Ryland & Austin, 1959), and in similar conditions at Shoreham, the species settles on test surfaces from May to October, reaching peak numbers during July or July–August (A. P. Austin and D. J. Crisp). Elsewhere the breeding season would probably be somewhat later.

Distribution

Widely distributed throughout the warmer waters of the world. Recorded from the south and south-west of the British Isles from Shoreham to Milford Haven, from docks and harbours, especially where the water is artificially warmed. Johnston (1847, p. 340) recorded *B. neritina* as a British species. However, four of his five specimens are, in fact, *Tricellaria peachi* (Busk) (Hastings, personal communication), while the other, listed for Scarborough, would seem, in view of the known British distribution, to be a mistaken locality. Hincks (1880) did not include *B. neritina* as British, but Marcus (1937) has quoted the erroneous Johnston records. Harmer (1897), in a note on newly recognized or rare British Polyzoa, did not mention *B. neritina* although his notes referred to the Plymouth area, and no mention is made in the Plymouth

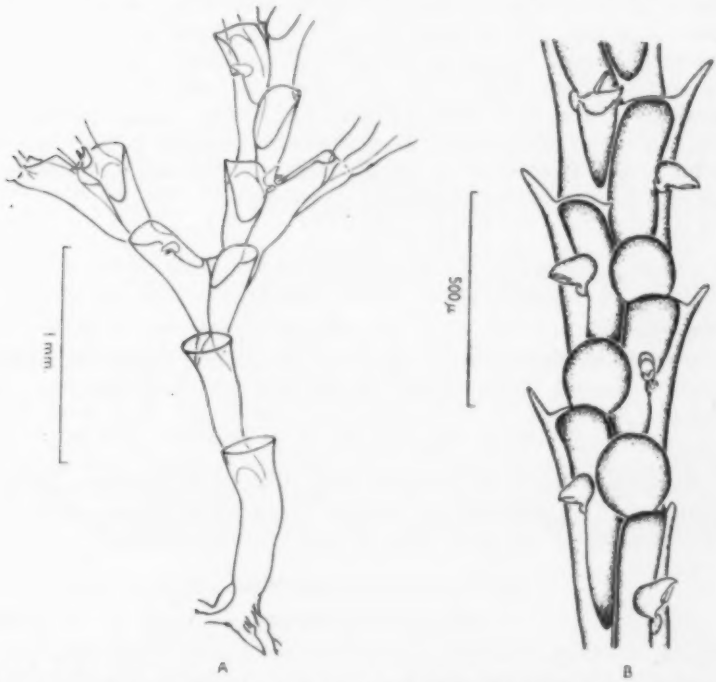

Fig. 4.—*B. plumosa*. A. Proximal part of colony showing the characteristic spineless ancestrula ; specimen from a settlement panel, Menai Bridge ; B.M.N.H. 1959.3.18.15. B. Frontal view of portion of branch ; Menai Straits, B.M.N.H. 1959.3.18.14.

Marine Invertebrate Fauna (Marine Biological Association, 1904). The first reference is that of Hasper (1912), although it is not perfectly clear whether his specimens were collected at Plymouth or not ; consequently the first definite British record is for 1928 (Marine Biological Association, 1957). (See Addenda).

B. PLUMOSA (Pallas)

Figs. 1 A (bifurcation), 2 E, F (avicularia), 4 A, B ; Pl. 2 F

Description

Zoarium up to about 8 cm. in height, composed of several feathery tufts rising from a tangled mass of radical fibres ; the branches disposed spirally around the central axis. The colour of the living zoarium buffish-orange. Branches narrow, with zooecia biserially arranged, dichotomously divided ; bifurcations of type 3 (Fig. 1 A). The zooecia slender, narrowing below, with the opesia occupying from three-quarters to almost the whole of the frontal surface. The outer margin produced distally to form a more or less pronounced unjointed spine ; the inner angle unarmed. Avicularia very small, less than the width of a zooecium, borne one-third to one-half of the distance down the outer margin of the opesia ; the beak slightly downcurved. Ovicells globular, slightly oblique to the axis of the zooecium ; aperture not conspicuous. Polypide with 14 tentacles. The ancestrula is very distinctive. The opesia is circular and faces distally ; no spines are present (Fig. 4 A).

A graceful species likely to be confused only with *B. stolonifera* or *B. purpurotincta*. From the former it is distinguished by its tall, feathery spiral colonies, the type 3 bifurcations, small avicularia, and the ancestrula. From the latter it is distinguished by its globular ovicells, small avicularia, and absence of a jointed spine on the outer distal angle.

Habitat

On stones, shells and boulders from shallow into deep water : occasionally on the shore. A common species on pier piles and floating pontoons.

Breeding

Embryos have been found from July to September ; significant settlement on panels immersed in the Menai Straits has only been recorded during September.

Distribution

On the eastern side of the Atlantic from Norway to Madeira ; also in the Mediterranean. Widespread and common in the southern part of the British Isles, but apparently replaced by *B. purpurotincta* in Scotland.

B. PURPUROTINCTA Norman

Figs. 2 D (avicularium), 5

Description

Zoarium composed of bushy tufts up to about 8 cm. in height ; purplish-red when dry. Zooecia biserially arranged ; bifurcations of type 3 (Fig. 1 A). Zooecia slender, narrowing below, with the opesia occupying most of the

frontal surface. A cylindrical jointed spine is borne on the outer distal angle ; below this the zooecium wall may be drawn out into a short projection (Marcus, 1940, Fig. 98) ; the inner angle unarmed. Avicularia about equal to the width

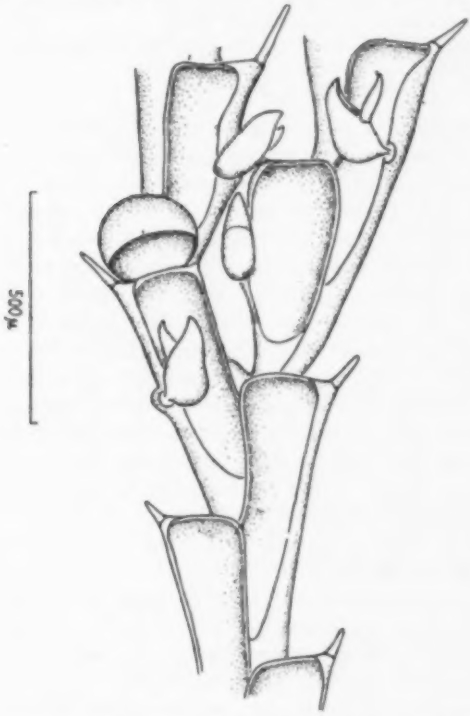

Fig. 5.—*B. purpurotincta*. Frontal view of bifurcation ; Shetland ; B.M.N.H. 1912.12.21.900.

of a zooecium, borne about one half way down the outer zooecial margin ; the beak slightly downcurved. Ovicells shallow, more or less hemispherical. Number of tentacles between 14 and 18 (Hincks, 1880).

B. purpurotincta was formerly confused with *B. plumosa* from which it is distinguished by its shallow ovicells, larger avicularia, and the jointed spine on the outer distal angle. From *B. stolonifera* it is distinguished by its bifurcations, the absence of a spine on the inner distal angle, and by the difference in the shape of the beak of the avicularium between the two species.

Habitat

From low-water mark to 274 m. (Marcus, 1940).

Distribution

A northern species found in Scotland and the north-east coast of Britain. Hincks (1880) also recorded it from the Menai Straits. Lo Bianco (1909) recorded *B. purpurotincta* from the Gulf of Naples, and the record is repeated by Friedl (1925), but this seems to be a case of wrong identification.

B. STOLONIFERA, sp. n.

Figs. 1 B (bifurcation), 2 G (avicularium, 6 A–E ; Pls. 1 C, 3 A, B

Synonomy. *Bugula* sp., Ryland & Austin, 1959.

Holotype. B.M.N.H. 1959.3.18.1. Collected by E. W. Knight-Jones, May 1958.

Type locality. Queen's Dock, Swansea, South Wales.

Paratypes. B.M.N.H. 1959.2.12.1 and 2 (spirit material), also specimens at the Marine Biology Station, Menai Bridge.

Description

Zoarium greyish-buff, 3–4 cm. high when well grown, not spiral but forming compact tufts. Three to five primary stolons—most usually a cruciform arrangement of four—arise from the ancestrula. These may grow long and spread over the substratum giving rise to other erect branching systems (secondary colonies) at intervals. Branches with zooecia arranged biserially, with bifurcations of type 4 (Fig. 1 B), and occasionally some type 3 in places. Zooecia long and slender, narrowing below, the opesia occupying one-half to three-quarters of the total length. Outer distal angle drawn out to form a spine-like projection, occasionally very large (Fig. 6 C) ; below it a slender spine. One slender spine is present on the inner distal angle, at right angles to the plane of the branch. In some colonies the spines are greatly reduced (Fig. 6 B), but some zooecia can be found showing the typical development of spines. Avicularia attached to the outer margin a little below the spines, their length about equal to the width of a zooecium ; beak downcurved. Ovicells sub-globular, the aperture conspicuous. Polypide with 13 or 14 tentacles. Ancestrula (Fig. 6 D) with one basal spine and three (rarely two) spines on each distal angle.

This species has been confused with *B. plumosa*, but well-grown colonies can be distinguished at a glance (Pls. 1 C & 2 F). Fragments of branches resemble *B. plumosa* in their delicate appearance, especially if the bifurcations happen to be of type 3, and the spines reduced. In any case, the spines may only be visible on close examination ; but the avicularia (Fig. 2), ovicells and, usually, the bifurcations provide certain means of separating the two species. In the 2 : 1 spine formula *B. stolonifera* resembles *B. avicularia*, but the latter is a larger, coarser species well characterized by its spiral growth and distinctive avicularia. Other, non-British, species resembling *B. stolonifera* are discussed on p. 97.

Habitat

The species is not sufficiently well known to give a full account of its normal habitat, but it has been found on pier piles, and once on a boat bottom. In the warm dock at Swansea, and in Milford Docks, it settles readily on immersed test surfaces.

Breeding

In Milford Haven the settling season in 1958 was from June to October, with a maximum settlement in August. In the Queen's Dock, Swansea, where the water is artificially warmed by a power-station effluent (Naylor, 1959 ; Ryland & Austin, 1959) the breeding season starts much earlier in the year. Settlement occurs from late April or early May to late October, and is heaviest during July or July–August (A. P. Austin).

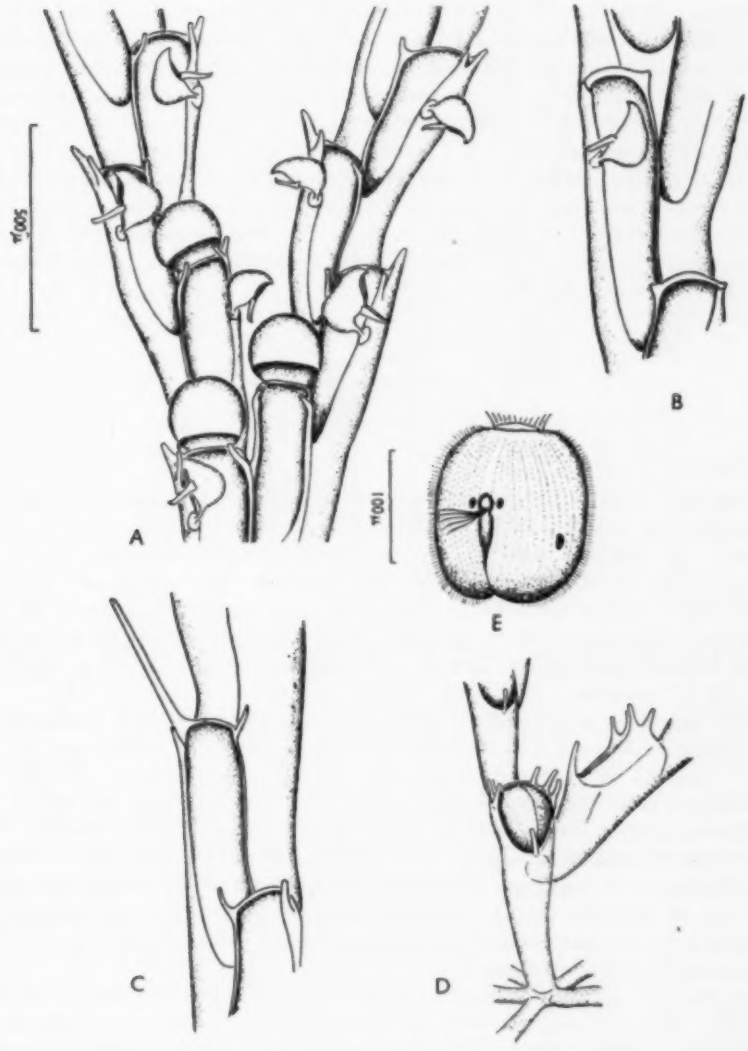

Fig. 6.—*B. stolonifera*. A. Frontal view of bifurcation ; holotype. B. Zooecia of a specimen from Miford Haven with reduced spines, B.M.N.H. 1959.3.18.3. C. Zooecia of a specimen from Milford Haven in which the outer distal spine is greatly developed, B.M.N.H. 1959.3.18.2. D. Ancestrula, from a settlement panel, Swansea Docks, B.M.N.H. 1959.3.18.4. E. Larva.

Distribution

Swansea Docks, Milford Haven (Milford Docks and Neyland) and Cóbh, Co. Cork. Some specimens, B.M.N.H. 1885. 12. 5. 3 and 4, which formed part of the Nolté Herbarium are referable to this species. The date of collection is unknown, but the Herbarium was purchased by the British Museum after Nolté's death in 1875 ; the specimens must have been collected prior to that date, and probably some years earlier. No precise locality is known, but the specimens are labelled " British coast " ; the label is not, however, supported by the register. If the label is correct the species would clearly not be a recent introduction ; but the evidence is too inconclusive to be certain.

Outside Britain *B. stolonifera* occurs in the Mediterranean, where it has been confused with other species (see p. 97), and specimens have been obtained from Marseilles and Naples.

B. AVICULARIA (Linnaeus)

Figs. 2 M (avicularium), 7 ; Pl. 1 A

Description

Zoarium bushy, of an orange-brown colour, 2–3 cm. high, the branches dichotomously divided and disposed spirally around the stem. Zooecia biserial ; bifurcations variable. Zooecia rectangular or narrowing below, the opesia occupying almost all of the frontal surface. Two spines on the outer distal angle, one on the inner. Avicularia large, longer than the width of a zooecium, with elongated downcurved beak, situated one-third to one-half of the distance down the outer wall of the opesia. Ovicells globular. Polypide with 13–15 tentacles.

The branches are usually biserial throughout the colony, although, as mentioned by Marcus (1950), specimens may be found in which three or four rows of zooecia occur distally, especially just below bifurcations. A specimen of this kind was referred to by Smitt (1867, p. 290 and 345–6, Pl. 18, fig. 11) as *B. avicularia* f. *flabellata*, and considerable confusion in the literature has resulted. Most authors, e.g. Hincks (1880) and Borg (1930), have assumed that the specimen was true *B. flabellata*, but Calvet (1900, 1902 a) considered it to be *B. sabatieri* (i.e. *B. simplex*) : in fact both views are incorrect, as examination has shown that the specimen, from the Gullmar Fjord, is true *B. avicularia*.

Habitat

On shells, hydroids and *Flustra foliacea* from between tidemarks to deeper water (100 m.).

Breeding

Lo Bianco (1909), at Naples, obtained larvae during October.

Distribution

Widely distributed around British coasts, but apparently not very common.

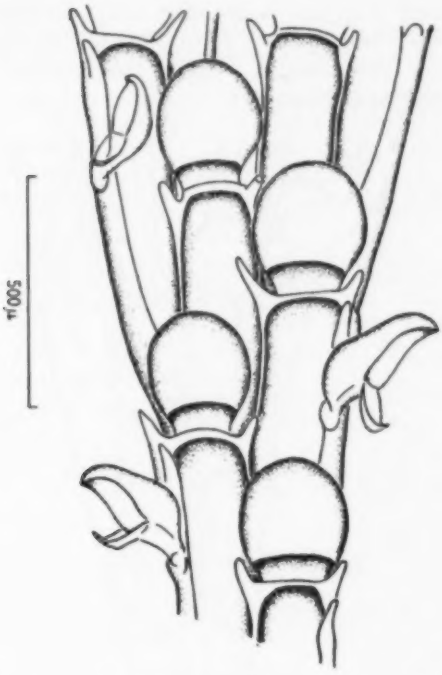

Fig. 7.—*B. avicularia*. Frontal view of bifurcation ; North Sea, B.M.N.H. 1959.3.18.11.

B. TURBINATA Alder

Fig. 2 I–K (avicularia), 8 ; Pl. 2 E

Description

Zoarium 3–6 cm. in height, consisting of several tufts arising from a common stock of fused radical fibres ; of an orange brown colour. Branches disposed in a spiral around the central stem. Zooecia usually biserial in the lower part of the colony, but becoming multiserial distally. Zooecia rectangular or narrowing proximally, the opesia reaching almost to the base of the zooecium. Each upper angle bears one spine, the outer one pointing distally, although Calvet (1900) records that specimens from the south of France may have two spines on the outer angle of the marginal zooecia. The avicularia are attached just below the spines on the outer wall of the zooecium, and are present on both inner and marginal zooecia, those borne by the latter being larger. The head is very rounded and, when seen from above, proportionally much broader than in any other British species. The beak is very short, and abruptly hooked. Ovicells more or less globular. Hincks (1880) gives the number of tentacles as 13, Calvet (1900) as 15–16.

B. turbinata is a very distinctive species at once recognized by its spiral growth and characteristic avicularia. Some specimens from the south of France show less tendency to be multiserial than the British material ; the

aperture of the ovicell is slightly wider than shown in Fig. 8 ; and the inner distal angle may bear two spines. Thus, although specimens from British localities have a 1 : 1 spine formula, it seems that formulae of 1 : 2 and 2 : 1 may occur in other parts of the range.

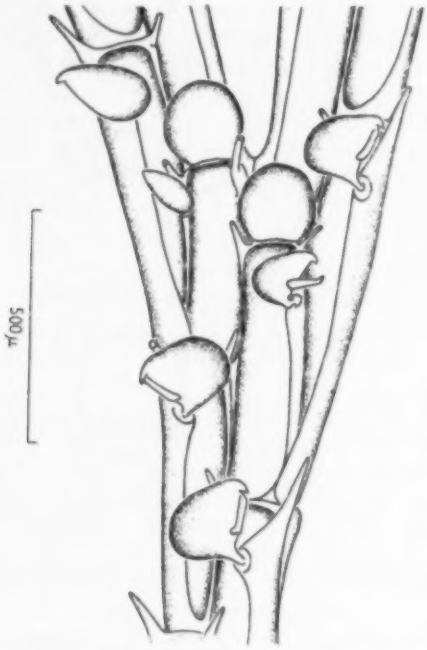

Fig. 8.—*B. turbinata*. Frontal view of bifurcation, Anglesey ; B.M.N.H. 1959.3.18.10.

Habitat

The only British species really characteristic of the littoral zone, it is found beneath rock ledges and in gullies near low water mark, and also in shallow water.

Breeding

In Britain (coast of Wales) embryos have been recorded during August and September, but at Naples Lo Bianco (1909) found larvae from February to May.

Distribution

Widely distributed in the southern part of the British Isles. Also present in the Mediterranean and Adriatic seas.

B. FLABELLATA (J. V. Thompson)

Figs. 2 A, B (avicularia), 9 A, B, C ; Pl. 2 A, D

Synonomy

Avicularia flabellata J. V. Thompson, MS., 1847.
Bugula flabellata (Thompson), Busk, 1852.

B. flabellata, Heller, 1867.
[*Non*] *B. avicularia* forma 2 : *B. flabellata*, Smitt, 1867 [= *B. avicularia* (L.)].
[*Non*] *B. flabellata*, Smitt, 1872, 1873 [= *B. simplex* Hincks].
[*Non*] *B. flabellata*, Verill & Smith, 1874 [= *B. simplex*].
[*Non*] *B. avicularia* forma *flabellata*, Waters, 1879 [= *B. calathus* Norman, Hastings, 1943].
[*Non*] *B. flustroides*, Verrill, 1879 a, 1879 b [= *B. simplex*].
B. flabellata, Hincks, 1880.
B. flabellata, Levinsen, 1894.
B. flabellata, Ortmann, 1894.
[*Non*] *B. flabellata*, Robertson, 1900 [= *B. pugeti* Robertson, 1905].
[*Non*] *B. flabellata* [*nec B. simplex*], Robertson, 1905 [see below].
[*Non*] *B. flabellata*, Osburn, 1912, 1914 [= *B. simplex*].
B. flabellata, Borg, 1930 [*partim* ; Fig. 83 is *B. simplex*].
[*Non*] *B. flabellata*, Grave, 1930, 1933 [= *B. simplex*].
B. flabellata, Calvet, 1931.
[*Non*] *B. flabellata*, Hasenbank, 1932 [= *B. calathus*, Hastings, 1943].
[*Non*] *B. flabellata* [*nec B. simplex*], Osburn, 1933 [see below].
[*Non*] *B. flabellata*, O'Donoghue & Watteville, 1935 [= *B. calathus*, Hastings, 1943].
B. flabellata, Marcus, 1938 [*partim* ; not Fig. 13 B, Marcus, 1949].
B. flabellata, Marcus, 1940.
[*Non*] *B. flabellata*, Richards & Clapp, 1944 [= *B. simplex*].
[*Non*] *B. flabellata*, Lynch, 1947, 1949 a, 1949 b, 1952, 1955 a, 1955 b, 1956 a, 1956 b, 1958 a, 1958 b [= *B. simplex*].
B. flabellata, Corrêa, 1948.
[*Non*] *B. flabellata*, Rogick & Croasdale, 1949 [= *B. simplex*].
[*Non*] *B. flabellata*, Osburn, 1950 [= *B. simplex*].
[*Non*] *B. flabellata* var. *acuminata* [*nec B. simplex*], Osburn, 1953 [see under *B. simplex*].
B. flabellata, Ryland, 1958 a, 1958 b.

Description

Zoarium forming a dense tuft 2–3 cm. in height, of a buffish colour when living, but becoming greyish when dried or preserved in spirit. Branches flabellate, dichotomously divided, somewhat circularly disposed. Zooecia in three to eight rows, oblong, of about equal width throughout their length. The opesia occupying all or nearly all of the frontal surface. The outer distal angles of the marginal zooecia bearing three spines, all the inner angles with two. The spines vary considerably in size and some of those on the outer zooecia may be very large. Avicularia are borne by zooecia of the inner and marginal series, those on the latter being considerably larger ; attached one-third to one-half way down the side of the opesia. The beak abruptly hooked. Ovicells sub-globular, with a moderately wide aperture. Polypide with 14 tentacles.

Although Hincks (1880) gave an adequate account of this species, it has been the centre of considerable confusion, and at least four other species seem to have been referred to *B. flabellata*. Some of these occur in British waters. *B. avicularia* f. *flabellata* (Smitt, 1867) was a form of *B. avicularia* in which some of the distal branches were triserial. *B. simplex*, which is common on the Atlantic coast of America, has there been called *B. flabellata* for nearly a century. The distinctive characters of the two species were pointed out recently (Ryland, 1958 a) and can be fully appreciated by comparing the descriptions given in the present paper. Further confusion has occurred between *B. flabellata* and *B. calathus*, but the avicularia provide a

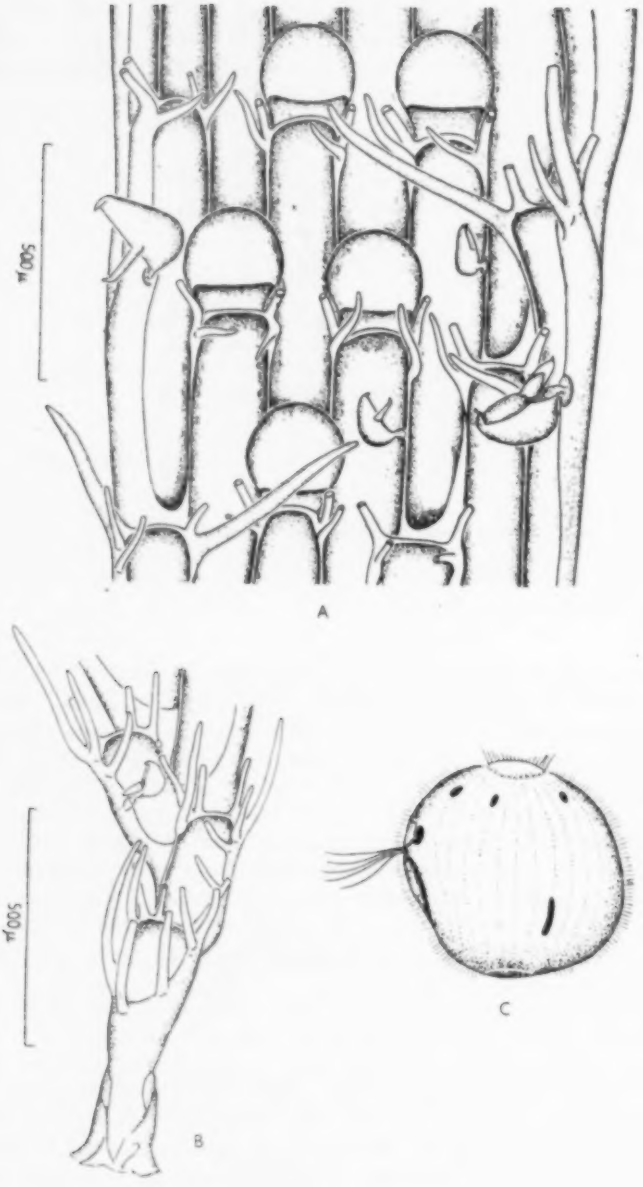

Fig. 9.—*B. flabellata*. A. Frontal view of part of branch, North Sea ; B.M.N.H. 1959.3.18.12. B. Ancestrula and proximal zooecia ; Menai Straits, B.M.N.H. 1959.3.18.13. C. Larva.

ready means of separation. As pointed out by Hastings (1943) the confusion may partly be due to an error in Hincks (1880, pp. 80–82) indicating that in Plate XI the illustrations of *B. flabellata* are Figs. 1–3, and of *B. calathus* Figs. 4–6. The explanation of the plate correctly shows that Figs. 1–4 refer to *B. flabellata* and 5–8 to *B. calathus*. The identity of *B. flabellata* Robertson (1905), and Osburn (1933) is uncertain. If the illustrations shown are accurate the lack of the hooked avicularium characteristic of *B. flabellata* must preclude them from this species. However, they do not belong to *B. simplex*.

The outstanding features of *B. flabellata* are the tufted habit, broad branches with many rows of zooecia, the large spines and, above all, the abruptly hooked beak of the avicularia. The last character can be seen as clearly on specimens from Brazil and Mauritius as on those collected around the British Isles.

Habitat

On stones, shells, *Flustra foliacea*, etc. from shallow to deep water. Occasionally found on the shore near extreme low water mark.

Breeding

Settlement has been recorded in September, and embryos have been noted from August to October (Menai Straits).

Distribution

In the North Sea and coasts of Europe from the Skagerrak to Portugal ; Atlantic coast of Morocco (Canu & Bassler, 1928) ; Mediterranean (Marcus, 1920) ; Adriatic (Heller, 1867 ; Marcus, 1920) ; Mauritius (specimen at the British Museum) ; Brazil (Marcus, 1938).

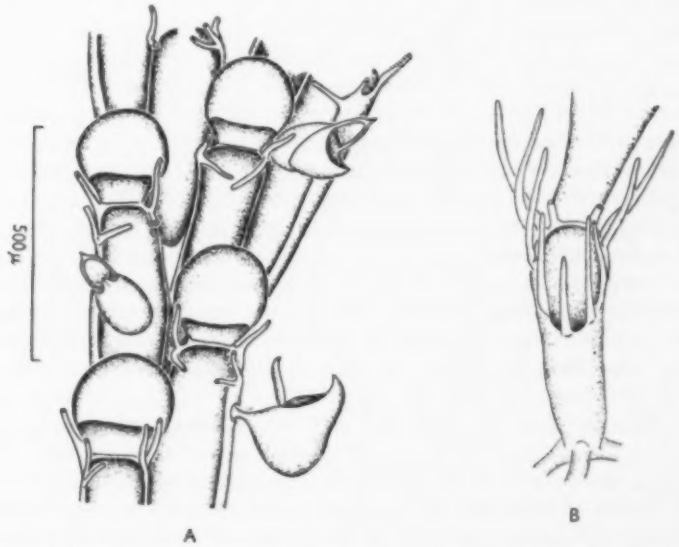

Fig. 10.—*B. fulva*. A. Frontal view of bifurcation ; holotype. B. Ancestrula, Milford Haven; B.M.N.H. 1959.3.18.6.

Hincks (1880) included Madeira in the range of *B. flabellata*, but no specimen exists and he gives no previous reference. Since this species is not mentioned in any of the papers on Madeiran Polyzoa, it seems possible that Hincks was misled by the reference to *B. ditrupae* Busk as *B. flabellata* var. *biseriata* (Busk, 1858 a).

B. FULVA, sp. n.

Figs. 1 D (bifurcation), 2 H (avicularium), 10 A, B ; Pls. 1 D, 2 B

Synonomy. *B. ditrupae*, Waters, 1897 [*partim*].
[?] *B. ditrupae*, Friedl, 1917.
Bugula sp. 1 Silén, 1950.

Holotype. B.M.N.H. 1959.3.18.5. Collected by J. S. Ryland from Menai Bridge pier.

Type locality. Menai Bridge, Anglesey, North Wales.

Paratypes. B.M.N.H. 1959.13.18.7. (Specimens in spirit from Milford Haven) ; further specimens from the type locality are held at the Marine Biology Station, Menai Bridge.

Description

Zoarium forming tufts, at first loose and somewhat cup-shaped, later more dense and bushy, 2–3 cm. in height. Colour of the living zoarium a yellowish-brown colour, turning grey when dried without fixation. Branches not spirally disposed. Zooecia arranged in two series, mainly with type 5 bifurcations (Fig. 1 D). In the distal part of the zoarium, branches may become quadriserial for some distance below a bifurcation ; in this case the bifurcation is simply a bisection of the branch. The zooecia are rectangular or slightly narrowed below with the opesia, except in the most proximal zooecia, occupying the whole of the frontal surface. Three spines are present on the outer distal angle, two on the inner. Where inner series zooecia are present, each distal angle bears two spines. The most distal of the spines on the marginal angles may be slightly larger than the others, but very large spines are absent. Avicularia are attached just below the spines on the external margin of the zooecia, their length somewhat exceeding the width of a zooecium. The beak is down-curved, often strongly so, but not abruptly hooked. Ovicells are sub-globular with a moderately wide aperture. Polypide with 13 tentacles.

Eleven spines are usually present on the ancestrula : three proximally, three at each distal corner and one on each lateral margin (Fig. 10 B). The spines on the proximal zooecia in a colony are intermediate in number between eleven and the normal complement of five. Stolons may arise from the base of the ancestrula, often three at 120° angles, with new colonies forming at intervals. The first zooecium in these daughter colonies resembles the ancestrula in appearance.

The affinities of this species are with *B. flabellata*, *B. calathus* and *B. aquilirostris*. From the first two, and to some extent from the last, *B. fulva* is distinguished by its biserial branches. The large spines and the hooked avicularia make *B. flabellata* very distinct, and *B. calathus* is well characterized by the large avicularia present on the marginal zooecia. *B. aquilirostris* differs from *B. fulva* in its larger and more numerous spines (although a very small third spine can sometimes be discerned on the inner upper angle of

zooecia of *B. fulva*), and in the larger numbers of avicularia. When inner zooecia are present in *B. fulva* they do not bear avicularia. Among species of *Bugula* not occurring in the British Isles those showing the closest resemblance to *B. fulva* are *B. ditrupae* Busk (p. 94) and *B. philippsae* Harmer (p. 96).

Habitat

The species has been found on the shore, both in the holdfasts of *Laminaria* and on the underside of large boulders where it occurs with *B. turbinata*. Its occurrence between tide-marks, however, does not seem characteristic. Typically it is found in shallow water, especially on pier piles and floating pontoons, but has not been obtained by dredging.

Breeding

The species settles readily on panels immersed for fouling studies. In the Menai Straits settlement on test panels in 1958 started in August, reached an immediate peak and then declined through September and October. Embryos have been found as late as 9th December.

Distribution

British Isles : Holyhead, Menai Bridge (Anglesey), Dale (Milford Haven), Plymouth, Poole, Harwich, Blyth (Northumberland). The earliest known specimen was collected by H. J. Waddington at Poole in 1909 and is now in the Waters Collection at the Manchester Museum. The next specimen, B.M.N.H. 1930. 1. 3. 17 was collected by A. B. Hastings at Plymouth in 1928, and further specimens, recognized as a distinct species, were collected there by L. Silén in 1949. Outside the British Isles the species occurs at Naples (see p. 96) and probably elsewhere in the Mediterranean.

B. CALATHUS Norman

Figs. 2 L (avicularium), 11

Synonomy. See Hastings (1943).

Description

Zoarium forming cup-shaped colonies, up to about 3 cm. in diameter. Straw coloured when living and horn coloured when dried : not becoming greyish. Zooecia multiserial (3–9 rows), equally wide throughout, the opesia occupying the whole of the frontal surface. Two spines are present on each distal angle, or three in the case of the outer angles of the marginal zooecia ; although in a specimen from Marseilles the formula was 2 : 2 throughout. Avicularia situated about one-third of the distance down the outer wall of the marginal zooecia ; very large and massive, their length equal to or exceeding the width of two zooecia ; beak downcurved. Much smaller avicularia may be present on some of the inner zooecia, but these appear to be very sparsely developed. Ovicells more or less globular, the aperture quite conspicuous. Calvet (1900) gave the tentacle number as fifteen.

While all the British specimens, and those from the south of France, that have been seen agree in detail with the above description, specimens from Naples and South Africa contained in museum collections differ in their avicularia. Those borne by the marginal zooecia are only a little longer than the zooecial width, while small avicularia appear to be present on all the inner

zooecia. This difference between size, numbers and distribution of avicularia in the two forms seems quite constant, and the two forms should, perhaps, be considered subspecies. The ancestrula of the second form has a central basal spine, one each side of the opesia and three on each distal angle (Waters, 1897).

Among British species, *B. calathus* most resembles *B. simplex* in its mode of growth, but in other respects is more like *B. flabellata*. The spine formula is

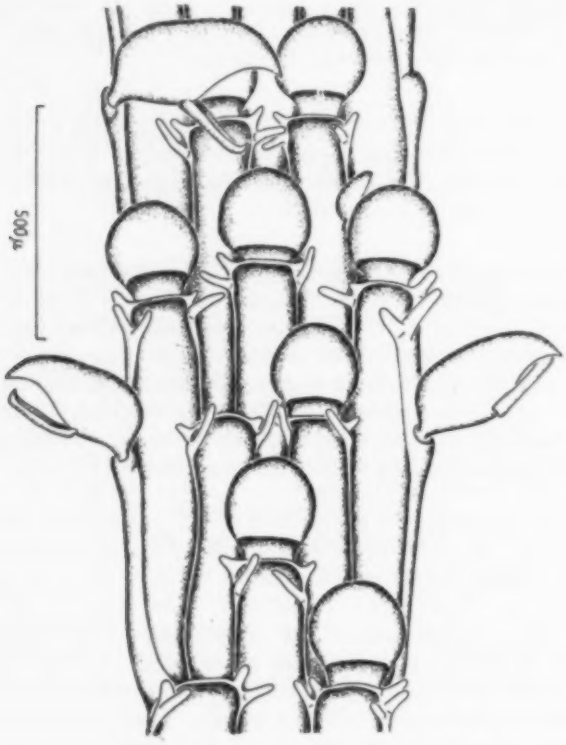

Fig. 11.—*B. calathus*. Frontal view of part of branch ; Bardsey Island, B.M.N.H. 1959.3.18.8.

the same in both, but the spines of the present species do not seem to reach the great size of those of *B. flabellata*. The shape of the avicularium provides a certain means of distinguishing the two species. The second form of *B. calathus*, with its smaller and more numerous avicularia, is more similar to well-developed *B. aquilirostris*. The latter differs in having a 3 : 3 spine formula on non-ovicellate zooecia, and the beak of the avicularium is quite different (Figs. 2 L and 12 B).

Habitat

B. calathus occurs between tide-marks and in shallow water.

Breeding

According to Lo Bianco (1909) embryos are found from July to October in the Gulf of Naples.

Distribution

In Britain confined to the south and south-west ; not common. Channel Islands ; south-west England ; Bardsey Island, Wales (Knight-Jones & Jones, 1956) ; Atlantic coast of Spain (Barroso, 1912) ; Mediterranean-Spain (Barroso, 1921, 1923), Balearic Islands (Barroso, 1922), France (Calvet, 1900, 1902 a, 1927 a, 1927 b), Italy (Waters, 1879, 1897) ; Adriatic (Hincks, 1886 ; Friedl, 1925) ; South Africa (Hastings, 1943). Kluge (1907) recorded *B. calathus* from the White Sea, but this was an error (*fide* H. Androsova).

B. AQUILIROSTRIS, sp. n.

Fig. 12 A, B

Synonomy. *B. ditrupae*, Hincks, 1886.
B. ditrupae, Waters, 1897 [*partim.*]
B. ditrupae, Marcus, 1937.

Holotype. Part of specimen, stained and mounted, B.M.N.H. 1959.1.20.1 ; the remainder, mounted dry, is contained in the Waters Collection at the Manchester Museum. Collected by H. J. Waddington at Bournemouth, 1908.

Description

Zoarium 1·5 cm. high, the dried material of a buffish colour. Branches flabellate, at first biserial but becoming quadriserial or more distally. Zooecia more or less rectangular, sometimes narrowing proximally, or weakly hexagonal. In the marginal zooecia the opesia occupies about three-quarters of the frontal surface, but in zooecia of the inner series it extends right to the lower margin. Each upper angle bears three spines, the most distal on each angle being suppressed when an ovicell is present. The distalmost spine on the outer angle of the marginal zooecia is larger than the other five. On the inner angles the two proximal spines arise together on the angle while the third is spaced a short distance along the distal margin. Avicularia present on every zooecium, situated about one-third of the way down the margin or sometimes lower on zooecia of the inner series. Those borne by the marginal zooecia are larger than those on the inner series, reaching about 250 μ in length, and somewhat exceeding the zooecial width. The rostrum is sharply and strongly downcurved, making the tip hooked like the beak of a bird of prey. The ovicells are more or less globular, with the aperture fairly conspicuous.

The affinities of this species lie with *B. flabellata*, *B. fulva* and *B. calathus*. From all of these it is distinguished by its 3 : 3 spine formula, and by the distribution and form of its avicularia. The avicularia of *B. flabellata* are characterized by having the tip of the beak abruptly hooked ; those of *B. calathus* by their very large size and the very sparse development of little avicularia on zooecia of the inner series. *B. fulva* is mainly biserial, and, in places where the branches are quadriserial, the inner zooecia do not possess avicularia. Also, in *B. fulva*, all the spines are of the same size.

Distribution

A specimen, now designated as the holotype, was collected by H. J. Waddington at Bournemouth in 1908. Part of this specimen is contained in the collection of the British Museum, and a larger portion of the specimen, which was sent to A. W. Waters, is now in the Manchester Museum. The species

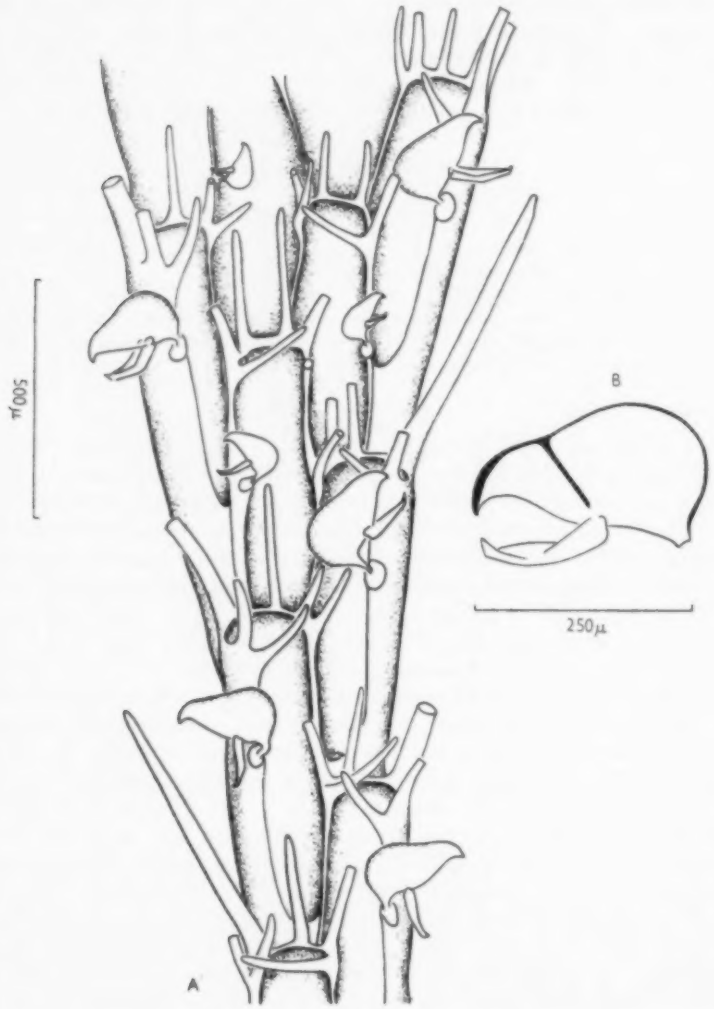

Fig. 12.—*B. aquilirostris*. A. Frontal view of part of branch ; holotype, B.M.N.H. 1959.1.20.1 B. Profile of avicularium from a marginal zooecium.

is represented in British collections by specimens from the coast of Portugal, from the Mediterranean and Adriatic seas, and from Brazil. It has been associated in the confusion between *B. ditrupae* and *B. fulva* (see p. 95).

B. SIMPLEX Hincks

Figs. 2 C (avicularium), 13 A, B ; Pls. 1 B, 3 A, B

Synonomy

[*Non*] *B. avicularia* forma *flabellata*, Smitt, 1867 [= *B. avicularia* (L.)].
B. flabellata, Smitt, 1872, 1873.
B. flabellata, Verrill & Smith, 1874.
B. flustroides, Verrill, 1879 a, 1879 b.
B. simplex, Hincks, 1886.
[*Non*] *B. simplex*, Waters, 1897.
B. sabatieri, Calvet, 1900, 1902 a.
B. flabellata, Osburn, 1912, 1914.
B. sabatieri, Marcus, 1920.
[*Non*] *B. simplex*, Friedl, 1917.
B. sabatieri, Friedl, 1925.
B. sabatieri, Harmer, 1926.
B. flabellata, Borg, 1930 [*partim* ; only Fig. 83 is *B. simplex*].
B. flabellata, Grave, 1930, 1933.
B. sabatieri, Neviani, 1937.
[*Non*] *B. simplex*, Neviani, 1939.
B. flabellata, Richards & Clapp, 1944.
B. flabellata, Lynch, 1947, 1949 a, 1949 b, 1952, 1955 a, 1955 b, 1956 a, 1956 b, 1958 a, 1958 b.
B. flabellata, Rogick & Cronsdale, 1949.
B. flabellata, Osburn, 1950.
B. sabatieri, Gautier, 1952.
[*Non*] *B. flabellata* var. *acuminata*, Osburn, 1953.
B. simplex, Ryland, 1958 a, 1958 b.

Description

Zoarium short, 1·5–3 cm. high, the branches all arising near the base of the very short stalk. Fan-shaped when very small, becoming funnel-shaped ; the older colonies more tufted. Light orange-brown or straw coloured. Branches narrow at their origin, becoming broader distally. Usually three to six series of zooecia, but according to Calvet (1900) up to 9-serial. Zooecia narrowing proximally, the opesia occupying the whole of the front. Each zooecium bears one spine on each distal angle ; very rarely two spines may occur on each angle. Marginal zooecia may have a spine formula 2 : 1. The spines may be well developed or quite reduced. Avicularia are present only on zooecia of the marginal series, borne about one-quarter way down the outer margin. The beak is downcurved, not abruptly hooked. Ovicells more or less hemispherical. The tentacle number is normally 13, but according to Calvet (1900) numbers of 12 and 14 may occur. The ancestrula has five spines, and about three short flat stolons radiate from it.

The characters of *B. simplex* make it so distinct that it is surprising that it should ever have been confused with *B. flabellata*. The spine formula, the ovicells, and the avicularia all provide a ready means of distinction. The var. *acuminata* (Osburn, 1953) seems to be a distinct species. The zoarium is

described as biserial, and the ovicells are globular, both characters disagreeing with the description of *B. simplex*. Also the locality, the Galapagos Islands, is outside the known range of *B. simplex*.

The original description (Hincks, 1886) was a poor one. This has lead to erroneous identifications by Waters (1897) and others, while the species was

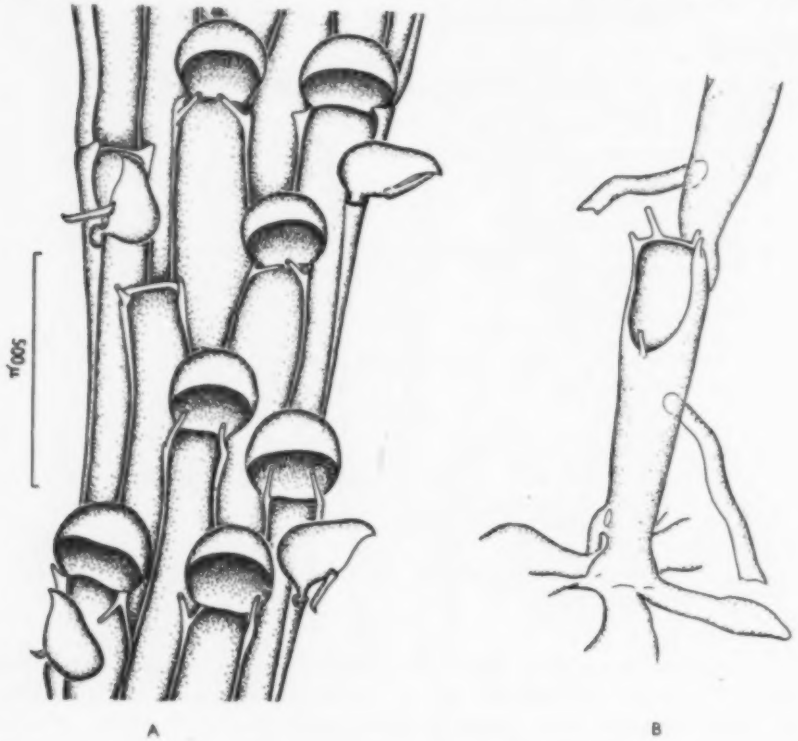

Fig. 13.—*B. simplex*. A. Frontal view of part of branch ; Holyhead, B.M.N.H. 1959.3.18.9 B. Ancestrula ; Milford Haven.

redescribed as *B. sabatieri* by Calvet (1900). Calvet was not correct in identifying *B. avicularia* f. *flabellata* (Smitt, 1867) with his species (see p. 80).

Habitat

In Britain *B. simplex* is best known through settlement on panels used for fouling studies. It has not been found by dredging. In America it is found mainly on pier piles and other submerged structures (Rogick & Croasdale, 1949), only rarely on algae. Calvet (1900) found it growing on *Zostera marina* at a depth of 1–6 m.

Breeding

Larvae have been obtained from specimens collected at Holyhead during September, October and November, but the first settlement on panels occurred

during August. In Milford docks settlement in 1958 took place from July to September (A. P. Austin).

Distribution

Recent British records are from Holyhead and Milford Haven. The earliest known specimen was collected at Lowestoft ; the actual date is unknown, but the registered number B.M.N.H. 1893. 8.18.1. indicates that it must have been prior to 1893. Outside Britain it is found on the east coast of North America from Florida to Maine (Osburn, 1914), in the Mediterranean (Calvet, 1900, 1902 a) and the Adriatic (Hincks, 1886 ; Marcus, 1920). The Waters Collection at Manchester includes a specimen collected and named as *B. sabatieri* by Calvet (see Ryland, 1958 a).

The larvae of British species

The larva of *B. neritina* (Fig. 3 B) differs slightly from that of the other species of *Bugula*. It is larger and has a pair of black, laterally placed pigment spots. In the other species a number of bright orange-red pigment spots may be found, and, in some cases at least, their number and disposition provide a useful taxonomic character. The maximum number appears to be five pairs in *B. fulva* and *B. flabellata* disposed as shown in Fig. 9 C. The two spots constituting the first pair are placed either side of the " plumet vibratile " ; the second, third and fourth pairs are spread round the upper hemisphere higher than the first pair and just below the " calotte " ; the fifth pair, greatly elongated, is situated in the lower hemisphere, lying below the space between the third and fourth pairs. The larvae of *B. fulva* and *B. flabellata* appear identical. *B. simplex* from the Mediterranean has eight pigment spots, corresponding in position to the first three and the fifth pairs in *B. flabellata* but lacking the fourth pair. The larva is described and figured by Calvet (1900). Larvae of *B. simplex* collected at Holyhead showed considerable variation in the development of pigment spots, and none showed the eight vivid spots described by Calvet. In some specimens none were visible, in some only the large pair in the lower hemisphere, in others the first pair by the " plumet vibratile " showed as well as the large lower ones, and, rarely, all four pairs could just be discerned. Larvae from American colonies have been described as lacking pigment spots (Grave, 1930), but some faint spots may be present (*teste* W. F. Lynch). The larva of *B. stolonifera* (Fig. 6 E) has two pairs of pigment spots corresponding to the first and fifth pairs of *B. flabellata*. In *B. plumosa* (Barrois, 1877) there are two pairs disposed as in *B. stolonifera*. The shape of the larva of *B. turbinata* resembles that of *B. fulva* and *B. simplex*, but there are no pigment spots (Calvet, 1900). Data about *B. purpurotincta*, *B. avicularia*, *B. calathus* and *B. aquilirostris* are lacking.

DISCUSSION : CONFUSION BETWEEN SOME SIMILAR SPECIES

The foregoing descriptions have been prepared to facilitate the identification of species of *Bugula* found around the British Isles. All the species can readily be distinguished here, but may, in other parts of the world, be confused with species not native to Britain. Reference to the literature and the examination of museum specimens during the preparation of this paper has shown that a great deal of confusion already exists. In fact, the muddle among the

Mediterranean and Adriatic species is so great that a thorough revision of the genus is required, although beyond the scope of this paper. Some of the non-British species involved are characterized below and compared with the British forms they most resemble.

B. DITRUPAE Busk

B. fulva and *B. aquilirostris* are both rather similar to *B. ditrupae*, and the three species have hitherto been confounded. That *B. fulva* and *B. aquilirostris* have not previously been recognized as distinct is largely due to the inadequate original description of *B. ditrupae*. Reference to the holotype in the British Museum (Natural History) has shown that the specific diagnosis (Busk, 1858 b) is poor, and the figure inaccurate in several respects. To allow a true comparison to be made between these species, a new description of *B. ditrupae* has been prepared making use also of the plentiful paratype material in the Museum.

Synonomy

Bugula flabellata var. *biseriata*, Busk, 1858 a.
B. ditrupae, Busk, 1858 b.
[*Non*] *B. ditrupae*, Hincks, 1886.
[*Non*] *B. ditrupae*, Waters, 1897.
[?] *B. ditrupae*, Calvet, 1907.
B. ditrupae, Norman, 1909.
[*Non*] *B. ditrupae*, Friedl, 1917.
[?] *B. ditrupae*, Calvet, 1927 a.
[*Non*] *B. ditrupae*, Marcus, 1937.

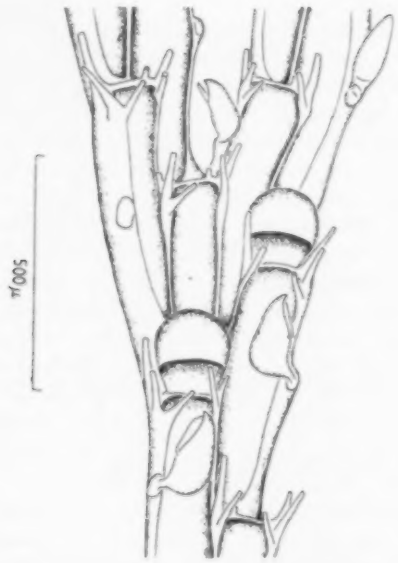

Fig. 14.—*B. ditrupae*. Frontal view of bifurcation; Madeira; paratype, B.M.N.H. 1912.12.21.877.

[?] *B. ditrupae*, Neviani, 1937.
B. ditrupae, Hastings, 1943.
[*Non*] *B. ditrupae*, Gautier, 1956.

Description

The branches divide dichotomously to form small, fan-shaped colonies measuring about 1 cm. in height. The zooecia are biserial, rarely tri- or quadriserial in distal regions, and bifurcations are of type 5 (Fig. 1 D). The zooecia narrow slightly proximally, and the opesia occupies all, or almost all, of the frontal surface. The usual armament of spines is three on each distal angle, but in the presence of an ovicell the inner angle may bear only two. Of the three spines one is usually longer than the other two, but this may be either the centre spine or the most distal. Avicularia are attached one-quarter to one-half way down the outer margin, their length being about equal to the width of a zooecium. The downcurved beak is slightly shorter than the head (Hastings, 1943, p. 428, Fig. 38 F). Ovicells are sub-globular with a wide aperture ; in appearance intermediate between *B. flabellata* and *B. simplex*. The ancestrula is provided with three proximal spines, and three on each distal angle. In one case the second zooecium had four spines on one of the distal angles, and proximal spines are frequently present on zooecia near the base of the colony.

Specimens from Madeira have invariably been associated with the serpulid worm *Ditrupa arietina* (O. F. Müller). The zoarium is usually attached to the calcareous tube of the worm just below the opening, and it has even been found on the operculum. This habitat character was stressed by Norman (1909) and is very constant ; yet, despite its obvious importance, it has been completely ignored by many workers. (Both Busk and Norman referred to the polychaete as *D. acuminata* with no further comment or details. However, it seems that this name rightly belongs to *Dentalium acuminatum* Deshayes. The genus *Ditrupa* was founded on *D. subulata* (Deshayes) originally wrongly placed in the genus *Dentalium*. *Ditrupa subulata* is a synonym of *D. arietina*, and I am grateful to Miss A. Edwards of the British Museum (Natural History) for confirming that the specimens on which *Bugula ditrupae* has been found are referable to this species).

Busk (1858 a, 1858 b) described the zooecia as fusiform, which clearly they are not: they are widest distally. The spine formula of the upper angles, outer quoted first, was given by Busk as 2–3 : 1. Since the number of spines on these angles is of considerable taxonomic importance, this is a most misleading statement : as stated above the correct formula is 3 : 2–3. The avicularia were stated by Busk to be attached below the middle of the zooecium although in his figure they were situated in the upper half. In the same figure the ovicells were shown as globular, whereas in fact their aperture is rather wide (Fig. 14).

Hincks (1886) referred a specimen from the Adriatic to *B. ditrupae*. He noted that the specimen did not agree fully with Busk's description of *B. ditrupae*, and gave the following account of the spines : " On the outer margin, which is somewhat folded in, are two spines, one of them suberect and pointing upwards, the other originating close to its base and curving slightly outwards.

A similar pair is placed at the top of the inner margin. Immediately behind the outer pair on the top of the cell [zooecium] is a tall spine of much stouter build than the rest, whilst another, of more slender proportions, rises about halfway between the lateral groups ". No intermediate spine has been seen in any of the specimens of *B. ditrupae* examined, and it is quite clear from his description that the specimens really belong to *B. aquilirostris*. This has been confirmed by examination of the specimens.

Waters (1897) recorded a biserial form from Naples and Capri with a 3 : 2–3 spine formula, and a quadriserial form from Trieste in which the avicularia of the outer zooecia were larger than those of the inner : both of these were assumed to be conspecific with the *B. ditrupae* of Hincks (1886). His specimens are, in fact, partly *B. aquilirostris* and partly *B. fulva*.

Friedl (1917) said of " *B. ditrupae* " from the Adriatic : " Ein ziemlich stark variierende Art ; von Hincks für die Adria angegeben. Ich konnte einige Kolonien in unbestimmten adriatischen Material vorfinden mit 2 Reihen von Zoözien und meist 3 Aussen- und 2 Innenrandstacheln." The spine formula quoted suggests that, in this case, *B. fulva* is the species in question, although it is not possible to be sure. Calvet (1927 a), Neviani (1937) and Gautier (1956) also refer to *B. ditrupae*, but the proper identity of their specimens remains uncertain.

A specimen, B.M.N.H. 1888.11.9.34, from Naples, was identified as *B. ditrupae* by Pergens. This specimen is *B. fulva*.

In view of the extensive confusion between these three species, the distinctive features of each are summarized below :

B. fulva. Biserial, sometimes quadriserial below distal bifurcations ; spines all about the same length, three on the outer angle and two on the inner ; avicularia borne just below the distal spines, the tip of the beak turned downwards ; not found on *Ditrupa arietina* tubes.

B. ditrupae. Biserial ; spines all about the same length, three on the outer angle and two or three on the inner ; avicularia borne halfway down the zooecial length, the beak pointed, and slightly downcurved ; ovicells with a wider aperture than either of the other species ; on *Ditrupa arietina*.

B. aquilirostris. Bi- or quadriserial ; spine formula 3 : 2–3, the uppermost spine of the inner group being spaced a short way along the distal edge of the zooecium and the uppermost spine of the outer group being longer and stouter than all the others ; avicularia borne one-third to two-thirds of the way down the zooecial margin, the tip of the beak curving sharply downwards ; not found on *Ditrupa arietina* tubes.

B. philippsae Harmer (1926) is rather similar to the above three species, but differs in the shape of the ovicells and, especially, in the possession of avicularia in which the beak is abruptly hooked.

B. SIMPLEX and *B. PLUMOSA* var. *APERTA* Hincks

Although it has now been shown that *B. simplex* is a distinct and well-defined species, the inadequacy of the original description (Hincks, 1886) has been responsible for much confusion. It is evident that Waters (1897) and later authors have confused it with *B. plumosa*. This explains why

B. simplex was redescribed by Calvet (1900) as *B. sabatieri*. *B. plumosa* var. *aperta* Hincks (1886) was described from the Adriatic, and differs from *B. plumosa* by having shallow ovicells. Waters (1897) suggested that in *B. plumosa* the ovicells develop simultaneously throughout the colony, and that var. *aperta* was merely a developmental stage. Because *B. simplex* also had shallow ovicells he considered that it was the same as var. *aperta*. His final conclusion, therefore, was that *B. simplex* and *B. plumosa* var. *aperta* were no more than synonyms of *B. plumosa*.

Waters, however, was not correct in his determination of specimens of *B. plumosa*. He described the ancestrula as having a spine on each upper angle and also a median basal spine. This is quite different from the ancestrula of *B. plumosa* shown in Fig. 4 A. The conclusion can be drawn from his papers that his specimens were, in fact, referable neither to *B. simplex* nor to *B. plumosa*. This has been confirmed by examination of the specimens in the Waters Collection at Manchester.

Friedl (1917) followed Waters' erroneous views. He mentioned that *B. simplex* had five or six rows of zooecia, but he still included it under *B. plumosa*. Marcus (1920) had true *B. simplex* from the Adriatic and not surprisingly called it *B. sabatieri*. Finally, Neviani (1939) listed both *B. sabatieri* and *B. simplex*, the latter only as a synonym of *B. plumosa*.

Some dried specimens of a biserial form from Naples, Nos. 1888.11.9.15 and 30, in the collection of the British Museum (Natural History) were referred to *B. simplex* by Pergens. The ovicells are shallow, but the avicularium is quite different from that of *B. simplex*. This is evidently the " *B. plumosa* " of Waters and others and may be the var. *aperta* of Hincks, but it is almost certainly specifically distinct from *B. plumosa*.

B. STOLONIFERA, *B. SPICATA* Hincks and some other species

A group of biserial species exists, not necessarily closely related, having in common an armament of three spines shared by the two distal angles. These require careful examination.

The original description of *B. spicata* Hincks (1886) is quite clear : " Generally biserial, but often quadriserial towards the upper part of the branches. Branches tall, much divided and sub-divided dichotomously, spreading. Zooecia in from 2 to 4 series, elongate, straight above, of about the same width throughout ; aperture occupying nearly the whole front, narrowing downward, the lower extremity pointed, a strong spike-like spine on the outer margin above, and two, placed one in front of the other, on the inner. Avicularia on the outer margin, almost close to the top, well rounded behind, beak short, the extremity shortly bent. Ooecium terminal, rounded, smooth."

Yet again the identity of this species has become quite obscure. Waters (1897) states : " We have *B. spicata* var. *aperta*, *B. spicata*, *B. plumosa* var. *aperta* and *B. plumosa*—all living side by side ; but if these are to be specifically separated it must be upon other distinctions than those at present indicated." But a comparison of the description of *B. spicata* with that of *B. plumosa* shows that they have little in common : *B. spicata* has a 1 : 2 spine formula, while in *B. plumosa* it is 1 : 0. Then he says : " . . . *B. spicata*

Hincks which I have biserial from Naples and Capri, while from Naples and Trieste it is 4-serial, and in these the outer avicularia are larger than the inner. The avicularia of *B. spicata* and *B. turbinata* are almost identical in shape ". Some, if not all, his specimens are in fact *B. turbinata*.

Equally unjustifiable is the confusion added by Calvet (1902 b). A specimen from Corsica is referred to *B. spicata* with the following description : " Cette espèce bien caractérisée par ses aviculaires capités et ses zoécies pourvues de trois épines dont deux externes et une interne, forme une colonie très grêle qui, dans l'échantillon de Pietranera, ne présente jamais plus de deux séries de zoécies ". Here the spine formula, 1 : 2 in the original description, has become 2 : 1, a highly important change. The *B. spicata* Calvet is clearly not the same species as that described by Hincks. However, Calvet's description could well apply to *B. stolonifera*, which is now known to be present in the Mediterranean. It should indeed be noticed that the 1 : 2 spine formula of *B. spicata* is a very unusual one, and should make that species readily recognizable. Some Mediterranean specimens of *B. turbinata*, however, have spines disposed in this way.

While the two instances of confusion discussed above seem unjustifiable, discrimination between the species that have a 2 : 1 spine formula requires considerable care. Excluding certain species easily distinguished by some obvious character, such as shallow ovicells in *B. cucullata* Busk, a group of six remains : *B. turrita* (Desor), *B. californica* Robertson, *B. germanae* Calvet, *B. pedata* Harmer, *B. avicularia* and *B. stolonifera*. For some of these the descriptions are not sufficiently complete to allow the construction of a key, but the principal characters of each are summarized in Table 2.

B. TURRITA (Desor)

B. turrita is probably the species meant by Hincks (1880) when he refers to *B. gracilis* var. *uncinata*. Of this he says : " I am unable to give any British locality for this species; but I have a specimen in my collection which was obtained on our coasts, and which I had wrongly referred to *B. plumosa*, until examination of fine examples of the same form from the United States directed my special attention to it ". To-day *B. turrita* is known only from the Atlantic coast of America, and it seems likely that Hincks was mistaken when he thought his specimen was of British origin. In case the species does occur in western Europe, and for the comparison with *B. germanae*, the following description is given (Fig. 15).

Zoarium up to 8 cm. in height, the branches spirally arranged ; bifurcations of type 3. Zooecia biserial, narrowed towards the base, the opesia occupying about two-thirds of the frontal surface. At the outer distal angle, the marginal wall curves inwards to form a short projection ; a true spine is present on the inner angle and on the outer side above the marginal denticle. The avicularium is small, and attached about half way down the outer margin of the opesia. The ovicell is globular and arises slightly to one side of the axis of the zooecium, and opens somewhat obliquely. The radicles sometimes develop anchor-like hooks, but these uncinate processes are not always present. The ancestrula resembles that of *B. plumosa* : indeed, the two species are

TABLE 2

Principal characters of some species of *Bugula* (see text).

	B. avicularia	*B. californica*	*B. stolonifera*	*B. pedata*	*B. turrita*	*B. germanae*
Form of zoarium	Spiral	Spiral ; sometimes 3- or 4-serial below bifurcations	Tufted, not spiral	Tending to become 3- or 4-serial distally	Spiral	
Extent of opesia	3/4 or more	2/3 or more	1/2-3/4	About 3/4	About 2/3	About 1/2
Bifurcations	Not uniform	Not uniform	Type 4, rarely type 3	Type 5 with some type 4 proximally	Type 3	Type 3
Position of avicularium on zooecial wall	Half way down or just above	Distal half	A little below the spines	Distal half	Half way down	Half way or more down the lateral wall of the opesia
Character of avicularium	Large, length exceeding zooecial width ; beak longer than head, strongly downcurved	Length about equal to zooecial width ; beak and head of about the same length	Length about equal to zooecial width ; beak shorter than head, strongly downcurved	Rather small, the beak short, pointed, with the extreme tip only sharply downcurved	Small, their length less than the zooecial width ; beak pointed, not strongly downcurved	Not known
Nature of proximal spine on outer angle	Finger-like ; true spine	Finger-like ; true spine	True spine, slender	True spine, delicate Some variation is found in the spine formula	A denticle formed by the inrolled margin	A denticle formed by the inrolled margin
Ovicells	Globular, aperture not conspicuous	Globular	Sub-globular, with a rather wide aperture	Unknown	Globular, slightly oblique to the axis of the zooecium ; aperture inconspicuous	Unknown
Special characters			Zooecia long and slender (see Table 1)	Numerous "pedate" radicles present, each turning at right angles and forming a dilatation on contact with substratum	Uncinate radicles may be present	Bases of zooecia C, E and D, F constricted just above their attachment to A and B respectively
Reference to descriptions	p. 78	Robertson, 1905 Marcus, 1937 Osburn, 1950	p. 78	Harmer, 1926	p. 98 Osburn, 1912	Calvet, 1902 b

very closely related. The species occurs on the Atlantic coasts of the North and South American continents, but, apart from the reference in Hincks

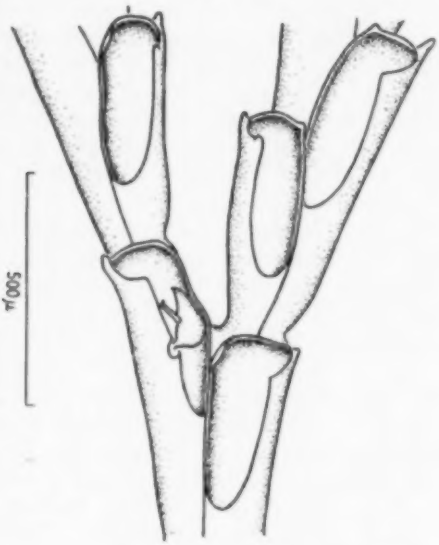

Fig. 15.—*B. turrita*. Frontal view of bifurcation. Woods Hole. Part of sample B.M.N.H. 1959.2.14.1.

(1880) quoted above, there are no records from the eastern Atlantic seaboard. *B. germanae*, from Corsica, does not appear to differ greatly from *B. turrita*.

SUMMARY

Eleven species of *Bugula* are known to occur in British waters, including three that have not previously been described. The characters of greatest value for separating these species are reviewed. Full descriptions are given of *B. neritina*, *B. plumosa*, *B. purpurotincta*, *B. stolonifera* sp. nov., *B. avicularia*, *B. turbinata*, *B. flabellata*, *B. fulva* sp. nov., *B. calathus*, *B. aquilirostris* sp. nov. and *B. simplex*. The account includes notes on habitat, breeding season and geographical distribution ; and a key is provided to facilitate identification.

B. ditrupae, from Madeira, is redescribed and compared with *B. fulva* and *B. aquilirostris*, as the three species have hitherto been confused. Synonomies of each are given.

The *B. simplex* of most authors is not that of Hincks, but another species : possibly the form known as *B. plumosa* var. *aperta*. *B. simplex* is the *B. flabellata* of most American authors, and the *B. sabatieri* of those writing on Mediterranean Polyzoa. Synonomies of *B. simplex* and *B. flabellata* are given.

A full description of *B. turrita* and summary descriptions of *B. californica*, *B. pedata* and *B. germanae* are given, and these species are compared with *B. stolonifera*. The characters of *B. spicata* are mentioned as it also has been confused with some of the above species.

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EXPLANATION OF PLATES

Plate 1

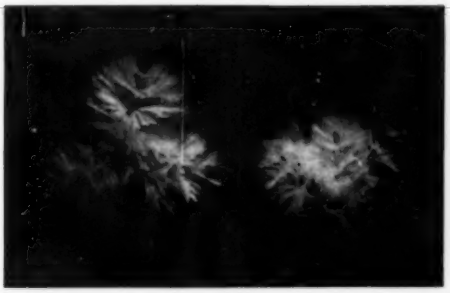
Species of *Bugula*. A. *B. avicularia*, North Sea ; B. *B. simplex*, Holyhead ; C. *B. stolonifera* sp. nov., Swansea ; *B. fulva* sp. nov., Milford Haven.

Plate 2

Species of *Bugula*. A. Young zoarium of *B. flabellata*, Menai Straits ; B. Young zoarium of *B. fulva* sp. nov., Menai Straits ; C. *B. neritina*, Swansea ; D. *B. flabellata*, North Sea ; E. *B. turbinata*, Anglesey ; F. *B. plumosa*, Harwich.

Plate 3

Bugula stolonifera sp. nov. and *B. simplex*. A. 10 × 10 cm. " Tufnol " panel after immersion for six weeks during August and September, 1958, in Milford Docks. The principal colonizer is *B. stolonifera* with a smaller number of zoaria of *B. simplex* ; the latter distinguished by their wider branches. Associated species on the panel are *Ciona intestinalis* (L.), *Ascidiella aspersa* (O. F. Müller), *Botrylloides leachi* (Savigny), *Diplosoma listerianum* (Milne-Edwards), *Elminius modestus* Darwin and *Mercierella enigmatica* Fauvel. B. *B. stolonifera* (centre and right) showing the development of creeping stolons from the ancestrula, and the way in which new erect branch systems arise at intervals along the stolons. In *B. simplex* (bottom left) the stolons are short and flattened.



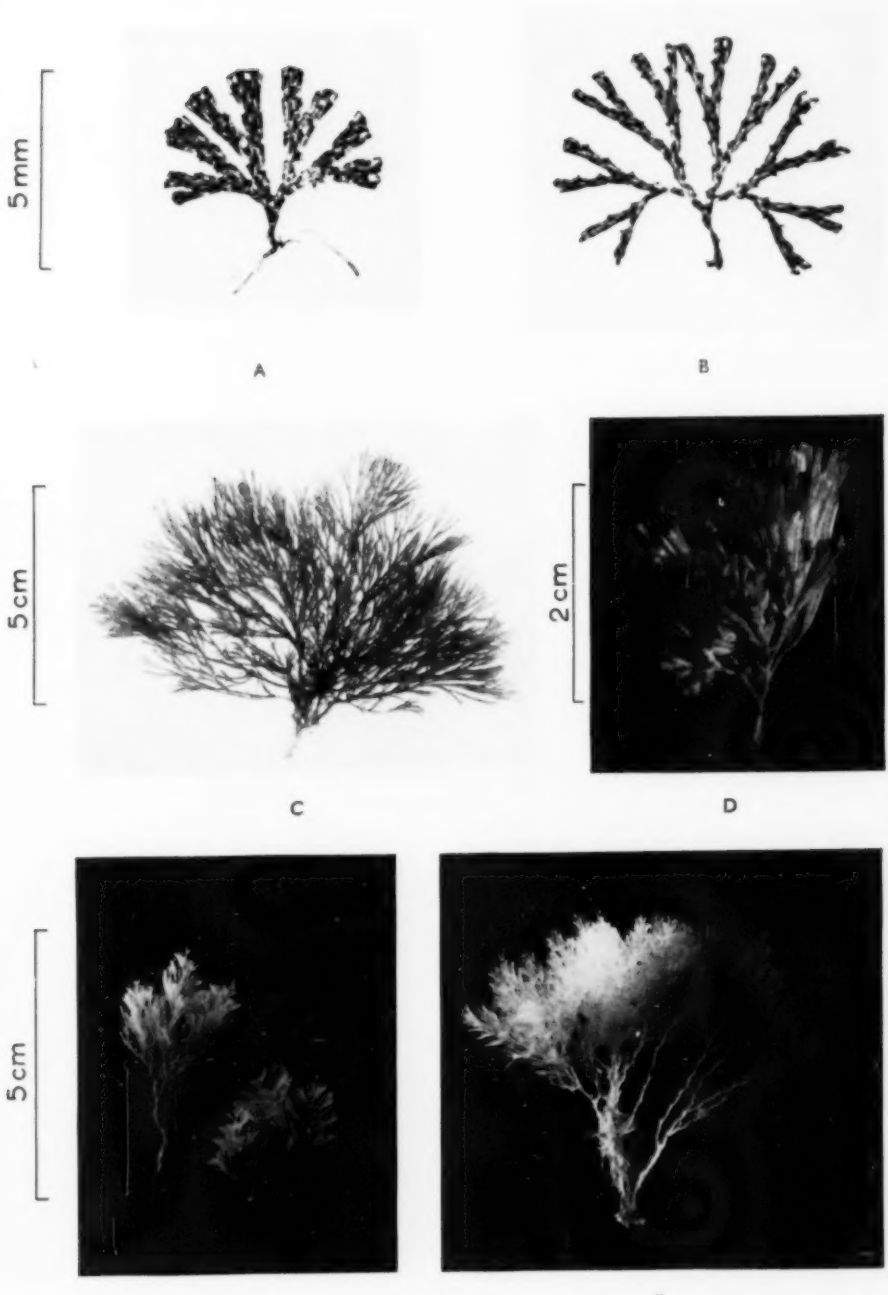
A

B

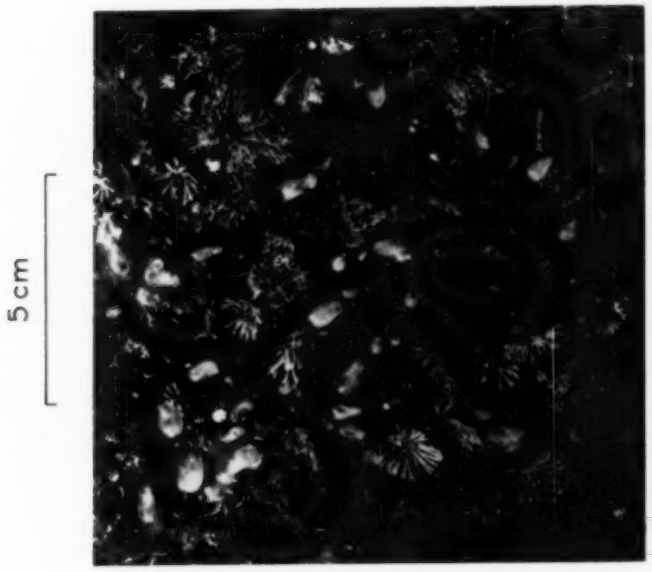
C

D

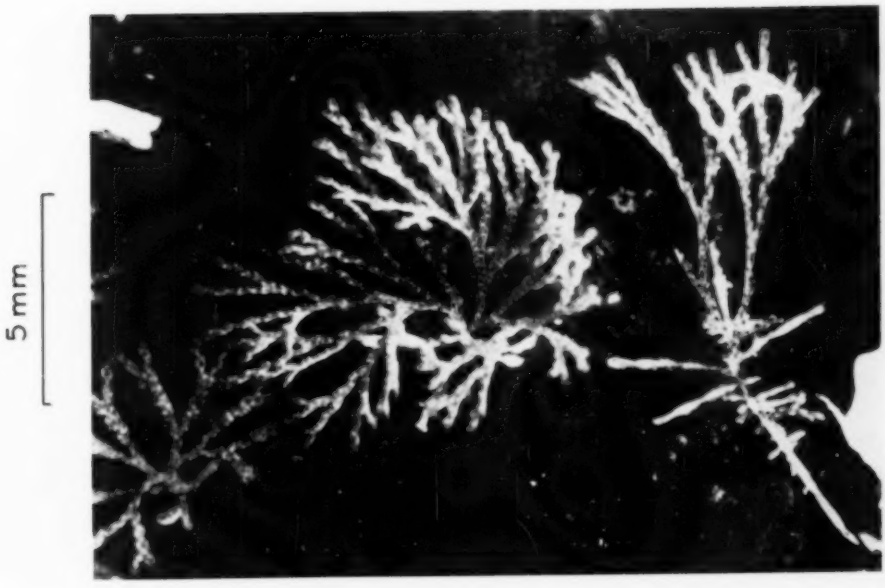
British species of *Bugula*.



British species of *Bugula*.



A



B

British species of *Bugula*.

ADDENDA

On p. 76 it was stated that, although the note by Hasper (1912) probably referred to Plymouth, the earliest definite British record for *Bugula neritina* was in 1928. A hitherto overlooked statement by Orton (1914) that "*Cellularia* [= *Bugula*] *neritina* grows into huge colonies in the inner basin at the Great Western Docks in a year" makes it almost certain that Hasper's record is in fact valid. This would put the discovery of *B. neritina* at Plymouth between 1904 and 1912.

Two recent papers by Maturo concern the genus *Bugula*. The first (1957) gave descriptions of *B. neritina*, *B. avicularia*, *B. turrita* and *B. californica*, and included a valuable statement on the size of avicularia. Settlement seasons were discussed in the second paper (1959).

Lynch (1959) referred again to *B. flabellata* where *B. simplex* was intended. The reader of Hyman (1959) should bear in mind the past confusion between the two species, which has naturally lead to a number of misleading statements in her book. Silén (1954) has recorded *B. flabellata* from off Rottnest Island, Australia, and the possibility of introduction on ships is suggested.

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ON THE LOCOMOTION OF THE MUD-SKIPPER *PERIOPHTHALMUS KOELREUTERI* (PALLAS) : (GOBIIDAE)

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(With 16 figures in the text)

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INTRODUCTION

The mud-skipper, *Periophthalmus koelreuteri*, is an outstanding example of a fish with amphibious habits and a high degree of locomotory specialization. But, despite the fact that the use of the pectoral fins for movement on land had been noticed by Martens as long ago as 1881, no critical study has been made of the various modes of locomotion exhibited by the fish.

The anatomy of the locomotory organs has received more attention. Grenholm (1923) has given a purely descriptive account of the pectoral and pelvic fin muscles in *P. koelreuteri*, and has revised the older descriptions given by Hämmerle (1898) and Hamburger (1904) for the same species. A comparative study of both the appendicular skeleton and the musculature of *Gobius caninus*, *Boleophthalmus boddaertii*, *P. schlosseri* and *P. chrysospilos* has been made by Eggert (1929), in order to trace the structural modifications that have led to the landward migration of gobid fishes. Lele & Kulkarni (1939) have described the skeleton of *P. barbarus*.

Concerning the locomotion of *Periophthalmus*, Martens (1881) noticed, during field observations in Borneo, that the mud-skipper levers itself along on its pectoral fins. He described the furrows made in the mud by the tail, but failed to notice the role played by the pelvic fins. A brief, but more accurate, account of the fish's movements on land has been given by Petit (1921) from his observations of *P. koelreuteri* in Madagascar. He noticed the role played by the pelvic and caudal fins, as well as the sequence of movements involved

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in locomotion on land. Harms (1929) has given a brief outline of the major morphological adaptations of *Periophthalmus* to land life, but without discussing either the modes or the mechanics of locomotion. Except for the use of the pelvic fins in climbing, Eggert (1929) does not discuss modes of locomotion in detail, and the general account of the fish's habits given by Champeau (1951) adds little to our understanding of its means of terrestrial progression. Inger (1952), in his description of the locomotory movements of *Periophthalmus*, erroneously regards the mechanism for skimming on the water's surface to be the same as skipping on land.

Specimens of *Periophthalmus koelreuteri* (Pallas) used in the following studies were obtained from mangrove swamps near Lagos, Nigeria. Dawson's Alizarin red 'S' method was used to prepare skeletal material. The musculature was investigated by direct dissection with the aid of a binocular dissecting microscope, and by means of serial histological sections. The action of certain

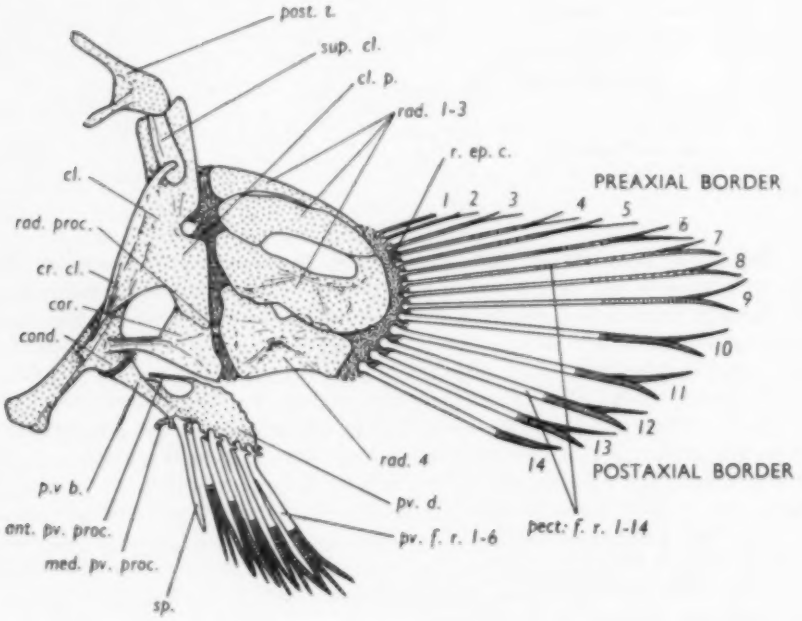


Fig. 1.—The appendicular skeleton of *Periophthalmus koelreuteri*. Lateral view of left pectoral girdle and fin, together with the left pelvic fin.

ant.pv.proc. anterior pelvic process *cl.* cleithrum ; *cl.p.* plate-like expansion of cleithrum ; *cond.* condyle of cleithrum ; *cor.* coracoid ; *cr.cl.* crista cleithralis ; *med.pv.proc.* medial process of pelvic dome ; *pect.f.r.* 1–14 rays of pectoral fin, 1 to 14 ; *post.t.* post-temporal bone ; *pv.b.* pelvic bone ; *pv.d.* pelvic dome ; *pv.f.r.*1–6 rays of pelvic fin, 1 to 6 ; *rad.* 1–3 : radials 1 to 3 of basal lobe ; *rad.*4 fourth radial ; *rad.proc.* radial process ; *r.ep.c.* epiphyseal cartilage of radials ; *sp.* spinous first pelvic fin ray ; *sup.cl.* supra-cleithrum.

muscles was confirmed by Faradic stimulation. Motion pictures have been used to study and analyse the fish's movements on land and on the surface of the water.

FUNCTIONAL ANATOMY OF THE LOCOMOTORY ORGANS

The appendicular skeleton

The high degree of locomotory specialization shown by *Periophthalmus koelreuteri* has involved extensive modification of the typical gobid appendicular skeleton. This has taken two trends. In the first place, considerable strengthening of the girdle and the fin rays has occurred to take the new stresses imposed by terrestrial progression. This strengthening is accompanied by an enlargement of the attachment areas of the major locomotory muscles (Fig. 1). The second trend in specialization has involved a lengthening of the basal lobe of the fin along its horizontal axis, in such a way that it projects from the body and carries the fin (i.e. the distal portion of the appendage consisting of the webbed fin rays) clear of the body (Fig. 2). Such an arrangement not only allows freedom of movement, but also increases the stride considerably.

The pectoral girdle of *P. koelreuteri* (Fig. 1) conforms to the description given by Eggert (1929) for *P. schlosseri*, and by Lele & Kulkarni (1939) for *P. barbarus*. As already pointed out by Eggert a strong *crista cleithralis* is developed along the anterior border of the cleithrum which, together with the

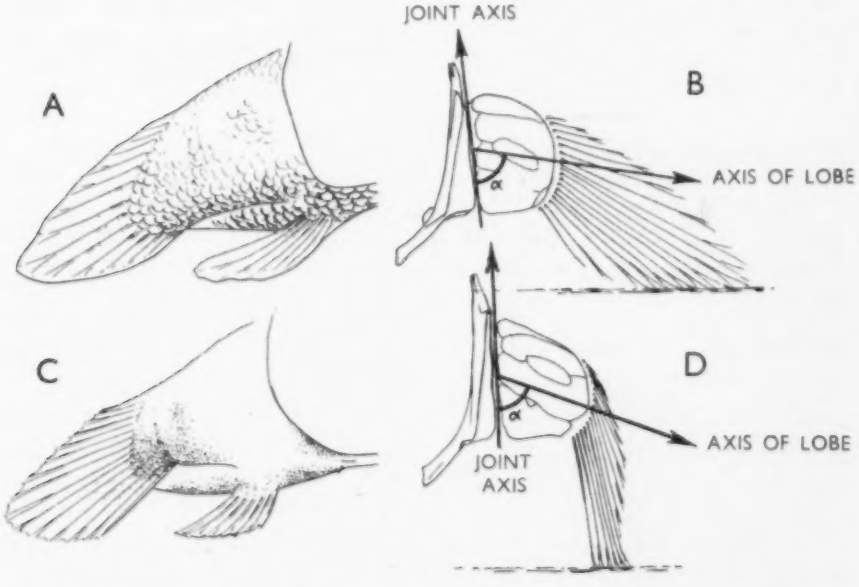


Fig. 2.—A. Pectoral fin of *P. schlosseri*. B. Skeleton of same, partly after Eggert. C. Pectoral fin of *P. koelreuteri*. D. Skeleton of same. Figs. B & D drawn from anterior with lobe fully abducted.

enlarged cleithral plate, serves for the attachment of the locomotory muscles. The condyle on the shaft of the cleithrum is of particular functional importance as it is the fulcrum about which the pelvic girdle rotates. The coracoid articulates with the cleithrum immediately above the condyle, and its area for muscle attachment is increased by a deep coracoid ridge lying in the horizontal plane.

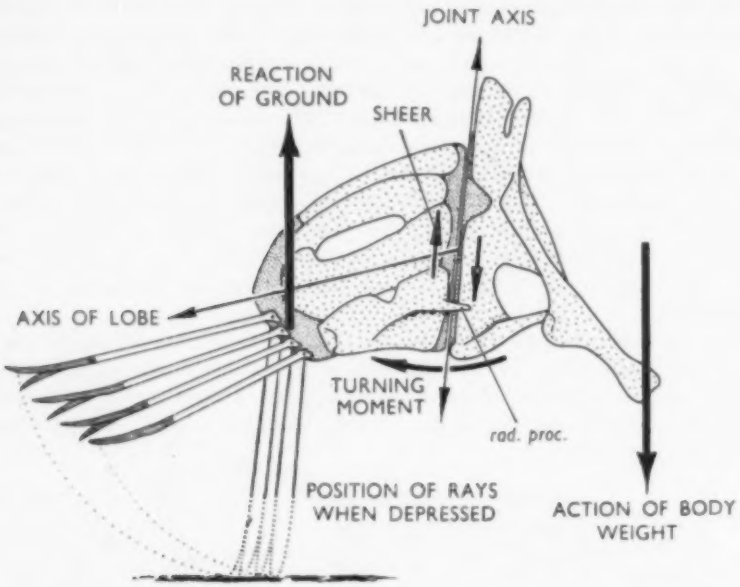


Fig. 3.—Diagram showing forces acting at the shoulder joint during locomotion on land, and the position of the pectoral fin rays when fully depressed. Posterior aspect.

The shoulder joint is a long hinge-like articulation, more or less vertically disposed. It is formed by the cartilaginous epiphyseal pad of the radials, and another pad of cartilage lying mesial to the plate-like expansion of the cleithrum and coracoid. This latter cartilage may be the unossified scapular, as suggested by Derjugin (1910). Movement of the joint does not appear to be restricted along its vertical axis by ligaments, although the two cartilaginous articular surfaces are separated by an intervening pad of fibrous tissue.

There are four radial elements forming the basal lobe of the pectoral fin. The preaxial radial is longer than the postaxial radial, consequently the axis of the fin is declined below the horizontal (Figs. 2 and 3). This enables the fin rays to be brought into a more effective position for transmitting their force to the ground, i.e., vertically downwards (Fig. 3).

In Table 1 a comparison of the relative lengths of the basal lobe is made between *Eleotris* sp., *Gobius caninus* and three species of *Periophthalmus*, calculated on the basis that the lobe in *Gobius* is of unit length. The angle of depression—i.e., the angle subtended by the lobe axis to the joint axis, is also given. The figures clearly show that *P. koelreuteri* has gone much further in

the process of lengthening and depressing the basal lobe than any of the other species, with the result that the fin rays can be brought much nearer to the vertical position (Fig. 2).

TABLE I

Comparison of fin lobes in various Gobiidae.

Species	Relative extension of lobe	Angle of depression
Eleotris sp.	1·04	100°
Gobius caninus	1·00	93°
P. schlosseri	1·77	75°
P. barbarus	2·09	78°
P. koelreuteri	2·11	70°

The rigidity of the basal lobe is increased by tongue and groove joints between the radials ; these are more highly developed between radials 3 and 4. There is no evidence in *P. koelreuteri* of fusion taking place between the radials as stated by Harms (1929) for *P. schlosseri* and *P. chrysospilos*. Harms correlates the increasing fusion of the radials with the efficiency of progression on land, but the fact that radial fusion does not occur in *P. koelreuteri* shows that this is neither a necessary modification, nor, indeed, a specific adaptation to efficient locomotion on land.

An opening between the second and third radials—the inter-radial fenestra, occurs in *P. schlosseri* and *P. koelreuteri*, but according to the figure of Lele & Kulkarni this structure is absent in *P. barbarus*. Another smaller opening is present between radials 3 and 4. The fourth radial is more heavily built and has on its inner side a horizontal ridge—the radial process, which passes mesially behind the coracoid (Fig. 3). The curved distal end of the basal lobe is capped with an epiphyseal pad of hyaline cartilage on to which the fin rays articulate.

The pectoral fins of *P. koelreuteri* possess fourteen pairs of fin rays each. There are no spinous rays in this species, although the proximal 2/3rds of each ray consists of a spine-like rod of fused lepidotrichia. The distal portion of each ray is composed of typical jointed lepidotrichia which, in the postaxial rays, are much shorter and compact. In rays 10 to 14 the proximal rods are specially thickened to take the weight of the body on land, moreover their respective lengths are so arranged that they are equidistant from the ground when fully depressed (Fig. 3). In this way the weight of the body is evenly distributed to the five or six postaxial rays.

A quantitative measure of stiffness is difficult to obtain, but the proximal parts of the pectoral and pelvic fin rays of *P. koelreuteri* are perceptibly stiffer than the corresponding structures in *P. schlosseri*, and hence are more highly adapted to support the weight of the body. The flexible extremities of the postaxial rays are functionally important in preventing the fin from sinking in the mud, as well as ensuring that the thrust of the fin is effective right to the end of its stroke. In *P. schlosseri* the distal portion of each ray is more divided and flexible than in *P. koelreuteri*. The pair of lepidotrichia forming each ray remain separate, although bound for most of their length with fibrous tissue.

The pelvic girdle movably articulates with the pectoral girdle through the

condyle on the cleithrum. This allows the pelvic girdle and fins to be raised or lowered as a whole.

The strut-like pelvic bones (Fig. 1, *pv. b.*) have their posterior end expanded mesially to form a dome shaped structure—the pelvic dome (Fig. 1, *pv. d.*). Anteriorly they articulate with the condyle. From the anterior end of the dome two slender processes pass forward along the dorsal edge of a cartilaginous pad which forms the posterior wall of the pericardium (Figs. 1, *ant.pv. proc.*; and 10 C, *cart.*). Another process passes forward inside the dome from the posterior extremity of the rim—the medial pelvic process (Figs. 1 & 10 D, *med.pv.proc.*). A transverse strip of cartilage joins the anterior tip of the medial pelvic process to the anterior lips of the pelvic dome (not shown in the figs.). The increase in height and size of the pelvic dome in *P. koelreuteri*, when compared with a purely aquatic gobid—such as *Eleotris*, can be correlated with the increase in musculature necessary to support the full weight of the body on the pelvic fins when out of water.

Basal elements are absent from the pelvic fins, each of which consists of an anterior spine followed by five stout fin rays of the semi-spinous type already described for the pectoral fins. The spine is formed from the fused lepidorichia. A curved process at the base of the ventral lepidotrichion, and a

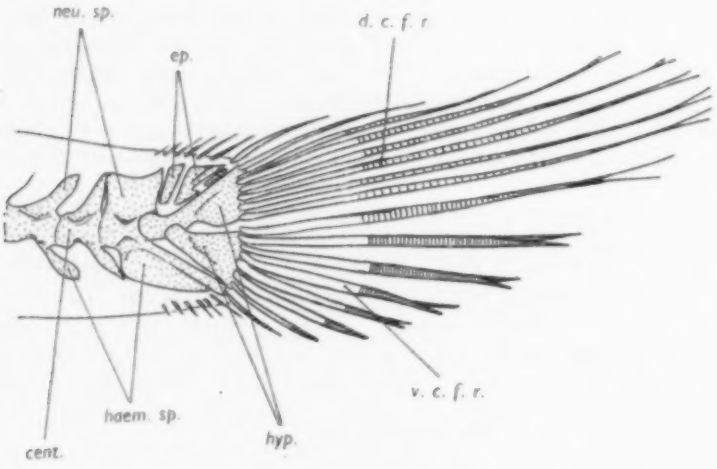


Fig. 4.—Caudal skeleton of *P. koelreuteri*.

cent. centrum; *d.f.r.* dorsal rays of the caudal fin; *ep.* epural elements; *haem.sp.* haemal spine; *hyp.* hypural elements; *neu.sp.* neural spine; *v.c.f.r.* ventral rays of caudal fin.

backwardly projecting uncinate process on the dorsal lepidotrichion of each ray, are important as points for muscle attachment (Figs. 1, and 10 A & B). The rays of the pelvic fins are arranged along the sides of the pelvic dome, rather than at the posterior border, as in *P. schlosseri* and *Gobius*. When fully

arrected, the pelvic fin rays form two converging rows of supports for the body in the case of *P. koelreuteri* (Fig. 1).

The lower border of the caudal fin is truncated. This is due to a shortening and thickening of the seven rays attached to the lower hypural bone (Fig. 4). The importance of this modification for skimming on the surface of the water will be discussed later, but it will be noted here that strengthening of the ventral rays is a mechanical necessity on land, both for supporting the tail region of the body, and for giving a firm point of attachment in the mud for the skip.

The musculature

Neither Grenholm (1923), describing *P. koelreuteri*, nor Eggert (1929), describing *P. schlosseri*, attempt to relate the action of muscle systems to the modes of locomotion. The full importance of the modifying effect that surrounding muscles have on the action of a particular muscle, especially when the pattern of activity is cyclic, has often been overlooked. Hence certain adaptive features of far reaching importance have been missed in previous accounts. For this reason it seems desirable that the musculature

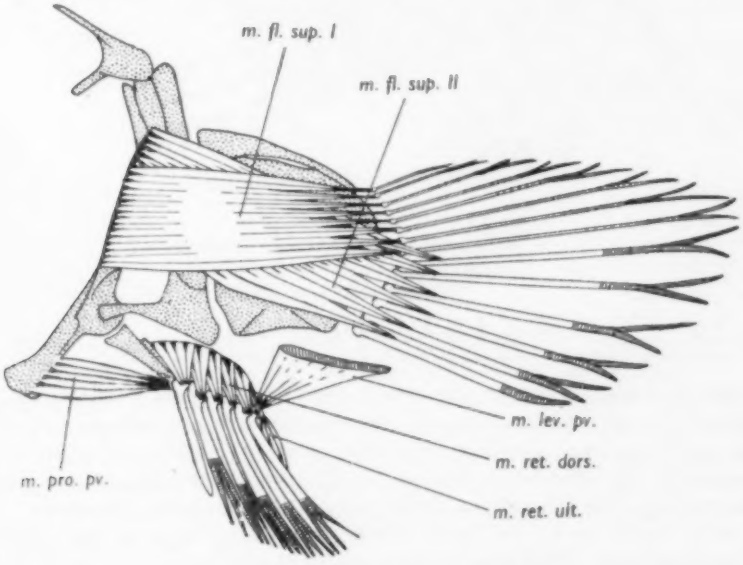


Fig. 5.—Flexor muscles of the pectoral fin.
m.fl.sup.I. musculus flexor superficialis I ; *m.fl.sup.II.* musculus flexor superficialis II ; *m.lev.pv.* musculus levator pelvis ; *m.pro.pv.* musculus protractor pelvis ; *m.ret.dors.* musculus retractor dorsalis ; *m. ret. ult.* musculus retractor ultimus.

of *P. koelreuteri* should be reconsidered from a functional point of view.

In the pectoral limb there are three muscles which, individually or collectively, cause flexion of the fin rays. Both Grenholm and Eggert refer to them

as abductors, although there are no direct abductors of the basal lobe itself. Besides flexing the rays, these muscles do indirectly cause abduction of the lobe, but only after the rays have been fully flexed and provided that the antagonistic action of the coraco-radial muscle does not prevent abduction.

The *Musculus flexor superficialis I* (Fig. 5, *m.fl.sup.I*) (abductor superficialis I of Eggert) originates from the middle of the *crista cleithralis* and inserts on to the proximal ends of the eight preaxial rays by tendinous slips. It flexes these rays. The direction of its fibres and their position of insertion make it a more efficient abductor of the lobe than the following two muscles.

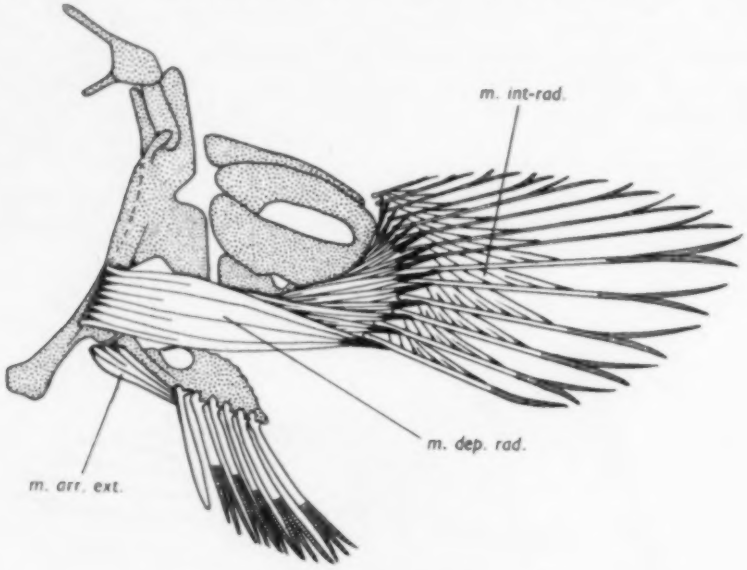


Fig. 6.—Depressor muscles of pectoral fin.
m.dep.rad. musculus depressor radiorum ; *m.int.rad.* musculi interradii.

The *Musculus depressor radiorum* (Fig. 6, *m.dep.rad.*) (abductor profundus of Eggert) has two portions. One originates from the lower part of the *crista cleithralis* and coracoid, and sends a strong bundle of fibres to the postaxial ray and the next three to it. The other more deep-seated portion originates from the 4th radial and fans out to the remainder of the rays. The depressor inserts on to the lower border of each ray a short distance from the proximal end. This muscle depresses all the fin rays, but also flexes the more ventral ones.

The *Musculus flexor superficialis II* (Fig. 5, *m.fl.sup.II*) (abductor superficialis II of Eggert) runs diagonally from the upper part of the *crista cleithralis* to the lower (postaxial) six rays, inserting on their dorsal sides a short distance from their proximal ends. This muscle both flexes and levates these rays, but when the rays are depressed below the axis of the fin, it causes depression and flexion. Thus, while the rays are above or parallel to the fin axis, this muscle

is antagonistic to the *M. depressor radiorum* ; depression and levation cancel out and only flexion results. But when the rays are below the fin axis the action of the two muscles summate and the rays are strongly depressed and flexed.

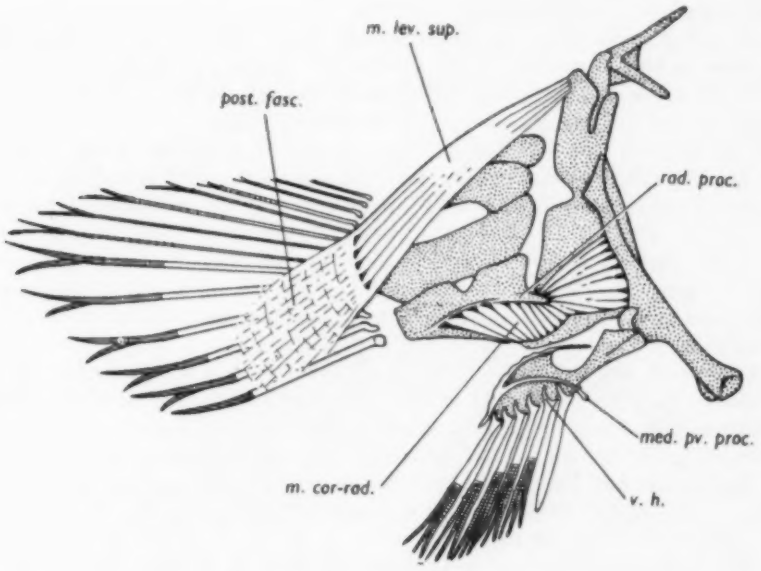


Fig. 7.—The coraco-radial muscle.

m.cor-rad. musculus coraco-radialis ; *m.lev.sup.* musculus levator superficialis ; *post. fac* fascia on posterior surface of fin; *rad.proc.* radial process ; *med.pv. proc.* medial process of pelvic dome ; *v.h.* ventral hook of pelvic rays.

The only muscle which acts as a direct adductor of the basal lobe is the *Musculus coraco-radialis* (Fig. 7, *m.cor-rad.*). This arises from the inner aspect of the coracoid, the ventral part of the cleithral plate and the corner of the cleithrum above the condyle. Its fibres pass out and insert on to the radial process and the lower part of the fourth radial. Besides its ability to adduct, this muscle is of fundamental importance to the terrestrial progression of *Periophthalmus* owing to its synergistic action in maintaining the stability of the shoulder joint.

During the period when the body is being lifted forward on the pectoral fins, the greater part of the body weight is transmitted through the shoulder joints to the fin rays. It has already been pointed out that these joints are more or less vertically disposed ; consequently sheering forces will be set up parallel to the joint axis by the weight of the body acting vertically downwards, and the normal action of the ground acting upwards through the fin rays (see Fig. 3). Fibres in the middle portion of the *M. coraco-radialis*, running parallel to the joint axis, would effectively oppose these sheering forces by their tension.

thus restricting or preventing any vertical displacement between the basal lobe and the girdle.

Other fibres of the *M. coraco-radialis* running at right angles to the joint axis, besides being efficient adductors, will oppose any tendency of the lower part of the joint to separate as a result of the couple set up between the body weight and its normal reaction.

Running diagonally from the dorsal tip of the cleithrum to the back of the fin there is the *Musculus levator superficialis* (Fig. 7, *m.lev.sup.*). It inserts on to the lower fin rays by a wide sheet of fascia. Its action is to levate the whole field of fin rays, but not the basal lobe of the fin.

The *Musculi interradii* are a group of muscles lying between and behind the fin rays (Fig. 6, *m.int.rad.*). Each takes a short origin from the postaxial border of one ray and fans out to a long insertion on the preaxial border of the ray below. The *M. interradii* are more developed at the back of the fin, where the fibres run across several rays to insert about half-way along the more ventral rays (Fig. 8). These muscles levate the fin rays, but in conjunction with their antagonist—the *M. depressor radiorum*, they cause the fin to be spread.

Occupying the inner side of the basal lobe there is the powerful extensor complex which provides most of the energy for locomotion on land. Eggert (1929) described this as three separate muscles in *P. schlosseri* : the adductor medialis, profundus I and profundus II. Three heads can be distinguished in *P. koelreuteri*, but the muscle as a whole is not differentiated to the same extent. All three portions have a common tendinous insertion on to the proximal ends of the fin rays.

The action of this muscle complex appears to involve a simultaneous extension of the fin rays, and adduction of the basal lobe. Eggert's identification of all three muscles as adductors is certainly not correct for at least one—the profundus II portion, is purely an extensor of the fin, and cannot cause any adduction of the lobe : this portion will be referred to as the *Musculus extensor profundus*. Both the medialis and profundus I portions run from the cleithrum to the rays, and therefore cause, either extension of the rays when the basal lobe is held still, or adduction of the lobe when the rays are held still, i.e., when anchored in the mud.

By studying motion pictures of a fish moving on land, taken from the dorsal aspect, it has been ascertained that the lobe is moved through an angle of approximately 50° during each cycle, whereas the excursion made by the fin rays is approximately 145°. From the commencement of the stroke, i.e., when the fin is fully flexed and the lobe abducted, adduction and extension take place simultaneously. But by the time the lobe is fully adducted, i.e., pressed against the side of the body, the rays have only described an arc of 75° ; thus, for the latter part of the stroke, only extension of the rays takes place until they have been swept through an angle of 145°. It has already been pointed out that the *M. coraco-radialis* is the only direct adductor of the basal lobe, therefore, since adduction of the lobe by Eggert's adductor profundus I seems to be a secondary rather than a primary activity, it is suggested that this muscle should be regarded as an extensor. It will be called the *Musculus*

extensor ventralis in view of the fact that it activates the ventral or postaxial field of rays. It is the main locomotory muscle used on land.

The medialis portion only supplies the upper or preaxial field of rays, and is not concerned in locomotion on land. Its function appears to be extension of the preaxial half of the fin whilst swimming.

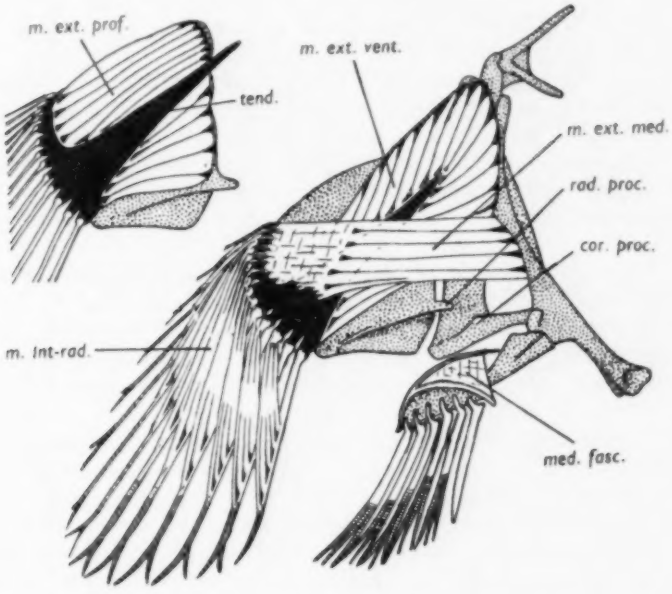


Fig. 8.—Extensor complex of pectoral fin. Inset shows deep extensor muscle.
cor.proc. coracoid process ; *med.fasc.* medial septum of fascia; *m.abd.med.* musculus abductor medialis ; *m.ext.med.* musculus extensor medialis ; *m.ext.prof.* musculus extensor profundus ; *m.ext.vent.* musculus extensor ventralis ; *m.int.-rad.* musculi interradii ; *rad.proc.* radial process ; *tend.* tendon.

The disposition of the three portions of the extensor complex are as follows :

(a) The *Musculus extensor ventralis* originates from the cleithral plate (Fig. 8, *m.ext.vent.*). It is unipennate in structure with short fibres inserting on to a wide strap-like tendon which passes mainly to the postaxial field of rays.

(b) The *Musculus extensor medialis* originates from the middle portion of the cleithrum (Fig. 8, *m.ext.med.*). Some of its fibres insert on to the tendinous strap, but others take a diagonal course upwards to insert on the upper rays by means of a wide sheet of fascia.

(c) The *Musculus extensor profundus* (Fig. 8, *m.ext.prof.*) originates from the inner aspect of the four radials, and inserts on to all the fin rays *via* the tendinous strap. The branch of the deep extensor, described by Eggert as originating on the outer side of the third radial and passing through the interradial fenestra in *P. schlosseri*, is much reduced in *P. koelreuteri*. In the

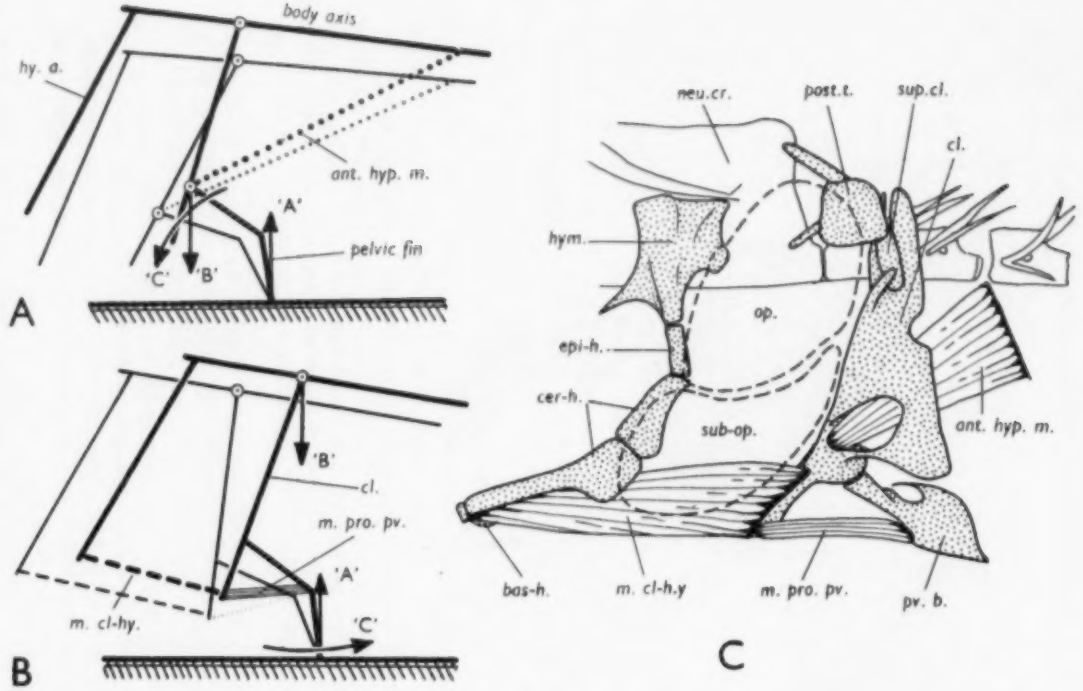


Fig. 9.—A & B. Diagrams to show the action of the muscles stabilizing the pectoral girdle. Movable joints are indicated by the symbol—○· Forces : 'A'—reaction of ground, 'B'—weight of body, 'C'—turning moment in the sense indicated. Thin lines indicate the relative positions of the structures after displacement by the turning force 'C'.

Diagram A : action of the anterior hypaxial muscle when the pelvic bones are free to rotate about the condyle of the cleithrum.

Diagram B : action of the *M. cleithro-hyoideus* when rotation of pelvic bones is prevented by the *M. protractor pelvis*.

Fig. 9, C.—The hyoid arch and pectoral girdle of left side. Showing the relative position of the extrinsic muscles to the girdle.

bas.h. basihyal ; *cer.h.* ceratohyal ; *cl.* cleithrum ; *epi.h.* epihyal ; *hy.a.* hyoid arch ; *hym.* hyomandibular ; *ant.hyp.m.* anterior bundle of the hypaxial musculature ; *m.cl-hy.* musculus cleithro-hyoideus ; *m.pro.pv.* musculus protractor pelvis ; *neu.cr.* neurocranium ; *op.* opercular bone ; *post.* post-temporal ; *pv.b.* pelvic bone ; *sub-op.* subo-perculum ; *sup.cl.* supracleithrum.

latter species it takes origin from the lower rim of the fenestra, and hence does not pass through the opening.

It will not be out of place at this point to consider the stability of the shoulder girdle. Locomotion on land by means of the paired fins demands a rigidity of the pectoral girdle sufficient to transmit the forward thrust of the fins to the body as a whole. The pectoral girdle, however, is not rigidly fixed to the axial skeleton, although its upper extremity is bound to the skull by a complex of muscles and ligaments, for the lower extremity is free to swing in an anterio-posterior plane (within the limits set by the ligaments of the pivot between the post-temporal and supracleithrum bones). This movement is controlled by two powerful extrinsic muscles of the girdle : the *Musculus cleithro-hyoideus* (Fig. 9, *m.cl-hy.*) which runs in an anterior direction from the lower part of the cleithrum, to its origin on the cerato- and basi-hyal bones of the hyoid arch ; and an anterior element of the hypaxial musculature (Fig. 9, *ant.hyp.m.*) which converges to a narrow insertion on the cleithrum above the condyle.

When the mud-skipper is moving on land by means of its paired fins, a forward thrust will be exerted on the cleithrum which will induce the lower end to swing forward. Such a movement would be opposed by the bundle from the hypaxial musculature. It is probable, therefore, that this muscle has a synergistic function in preventing forward movement of the cleithrum during locomotion.

On the other hand, it will be seen from Fig. 9 A & B, that the point around which the cleithrum pivots is anterior to the pelvic fins. Thus when the body is being supported by the pelvic fins only (and this happens during the recovery phase of each cycle) the cleithrum will be subjected to other turning forces.

If, in the first place, the pelvic bones are considered free to rotate about the condyle (Fig. 9 A), then the couple formed by the normal reaction of the ground ' A ' and the weight of the body ' B ' will tend to twist the pelvic bones anticlockwise, and the cleithra clockwise, ' C '. It has already been pointed out that the anterior hypaxial muscle will check or oppose this turning. But if rotation of the pelvic bone is prevented by the *M. protractor pelvis*, the cleithrum and the pelvic girdle can be considered as one rigid structure pivoted about its upper extremity (Fig. 9 B). In this case the couple formed by the body weight ' B ' and the normal reaction of the ground ' A ' will induce a turning moment in an anticlockwise direction ' C ', which would cause the fish to roll forward on its pelvic fins. It would be equally true to say that this couple caused the pelvic fins and cleithrum to swing backwards (anticlockwise) with respect to the body axis. Such a tendency would be opposed by the *M. cleithro-hyoideus* which braces the pectoral girdle to the skull through the hyoid arch.

From this discussion it will be seen that the stability of the girdles during locomotion on land is largely dependent upon the synergistic action of the anterior hypaxial bundle, the *M. cleithro-hyoideus* and the *M. protractor pelvis.*

The pelvic bones and fins can be raised or lowered as a whole by two pairs of muscles. The *Musculus levator pelvis* (Figs. 5 & 10 D, *m.lev.pv.*) lifts the girdle and the fins. It has a narrow insertion on the posterior tip of the

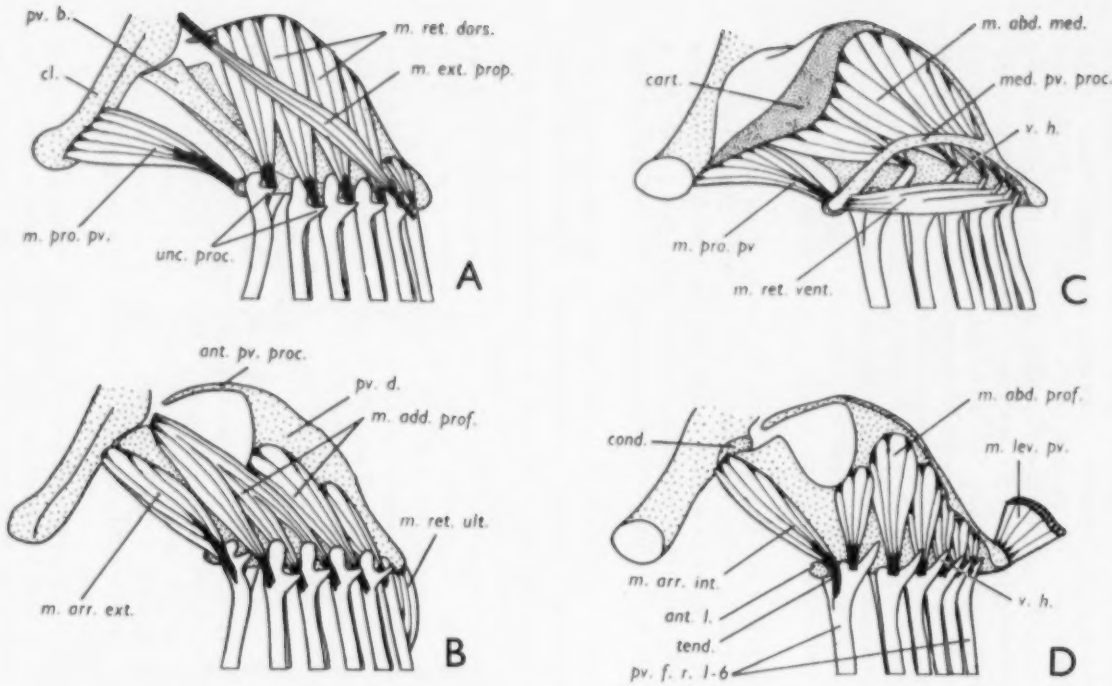


Fig. 10.—Musculature of the pelvic fin and girdle. Lateral views : A & B external, C & D internal aspect.
ant.l. anterior lip of pelvic dome ; *ant.pv.proc.* anterior pelvic process ; *cart.* pad of cartilage between anterior pelvic processes ; *cl.* cleithrum *med.pv.proc.* medial pelvic process ; *m.abd.med.* musculus abductor medialis ; *m.abd.prof.* musculus abductor profundus; *m.add.prof.* musculus adductor profundus ; *m.arr.ext.* musculus arrector externus ; *m.arr.int.* musculus arrector internus ; *m.ext.prop.* musculus extensor proprius ; *m.lev.pv.* musculus levator pelvis ; *m.pro.pv.* musculus protractor pelvis ; *m.ret.dors.* musculus retractor dorsalis ; *m.ret.ult.* musculus retractor ultimus ; *m.ret.vent.* musculus retractor ventralis ; *pv.b.* pelvic bone ; *pv.d.* pelvic dome ; *pv.f.r.*1–6 pelvic fin rays 1 to 6 ; *tend.* tendon ; *unc.proc.* uncinate process ; *v.h.* ventral hook of pelvic fin rays.

dome, from which the fibres fan out towards their origin in the fascia of the hypaxial musculature. The *Musculus protractor pelvis* (Figs. 5 and 10 A & C, *m.pro.pv.*) depresses or protracts the whole pelvic structure. It originates from the ventral extremity of the cleithrum and passes back to its insertion on the anterior lip of the rim, just in front of the spine, and the cartilaginous bridge between the lip and the medial pelvic process.

As already noted above, the *Musculus protractor pelvis* will act as a synergist or tension member, preventing rotation of the pelvic bones about the condyles, when the pelvic fins support the body. It will also act as a shock absorber when the fish lands after a skip. It is probable that the *M. protractor pelvis* assists skipping by contributing to the vertical component of the force required to lift the body.

A tendency for the pelvic fin rays to be arranged more to the side of the dome in *P. koelreuteri*, rather than at the posterior end as in other species, has led to a number of changes in the action of pelvic muscles. In discussing pelvic fin movements, lifting of the rays in a plane at right angles to the body axis will be referred to as adduction, while movement in the horizontal plane towards the body axis will be termed retraction. Certain of the muscles, however, effect a combination of these two activities, i.e., a simultaneous adduction and retraction. Simultaneous abduction and protraction, which causes the rays to be drawn forward in a vertical row, will be termed arrection.

Muscles of the pelvic fins may be divided for convenience into two groups : those lying external or dorsal to the dome, and those internal or ventral to this structure.

A superficial strap-like muscle, the *Musculus extensor proprius* (Fig. 10 A, *m.ext.prop.*), runs diagonally across the other muscles from the pelvic bones to an insertion on the sixth ray. This muscle twists the last ray slightly upwards and outwards as shown in Fig. 12, frames 35 and 36.

Covering the dorsal surface of the dome there are two muscles referred to by Eggert as the adductor superficialis and adductor profundus. The former takes a more dorsal origin and inserts on the uncinate processes of rays 1–5. Its action is a simultaneous adduction and retraction of the rays, or, in conjunction with its antagonists, a powerful retraction of the rays. It probably plays an important role in movement on land, and for this reason the name *Musculus retractor dorsalis* is to be preferred (Fig. 10 A, *m.ret.dors.*). Underneath this muscle there is the *Musculus adductor profundus* (Fig. 10 B, *m.add.prof.*) which takes its origin from the dorsal aspect of the pelvic bones and the dome, and inserts by tendinous slips on the anterio-lateral face of rays 2–6 a short distance from their proximal ends. The *Musculus arrector externus* (Fig. 10 B, *m.arr.ext.*) originates anteriorly on the pelvic bone, and inserts on the anterior border of the spine. It pulls the spine forward, and hence spreads the whole fin. The *M. arrector externus* may be regarded as a specialized portion of the *M. adductor profundus* supplying just the spine.

The muscles causing abduction and retraction of the fins are situated on the ventral side of the dome. The *Musculus retractor ventralis* (Fig. 10 C, *m.ret. vent.*) takes its origin from the cartilaginous bridge which spans the anterior lips of the dome. The fibres pass back to insert on the tips of the ventral

hooks belonging to rays 3–6, the largest bundle going to ray 5. This muscle was referred to by Eggert as the adductor superficialis I, but in *P. koelreuteri* it only causes retraction, not abduction. The abductor superficialis II of Eggert is a more deeply situated muscle which, in *P. koelreuteri*, originates from the medial septum, hence the name *Musculus abductor medialis* would seem more appropriate (Fig. 10 C, *m.abd.med.*). The medial septum is a sheet of fascia extending vertically from the medial pelvic process up to the dome (Fig. 8, *med.fasc.*). The *M. abductor medialis* inserts by tendinous slips on to the tips of the ventral hooks of all six rays, and causes a simultaneous abduction and retraction of the fin. On land its retractor function is probably of greater importance. A direct abductor, the *Musculus abductor profundus* (Fig. 10 D, *m.abd.prof.*) originates from the inner wall of the dome, and inserts on the proximal ends of all six rays. This muscle is not mentioned by Eggert for *P. schlosseri* or *P. chrysospilos*, but he may have included it in his abductor superficialis II.

The *Musculus arrector internus* (Fig. 10 D, *m.arr.int.*) effects a simultaneous abduction and protraction of the spinous first ray, and hence causes arrection of the whole fin. It arises anteriorly from the inner side of the pelvic bone, and inserts by a tendinous strap on the internal (ventral) side of the spine. The tendon passes round the anterior lip of the dome and in this way alters the direction in which the muscle pulls by about 30–40°. This arrangement increases the abducting action of this muscle.

The *Musculus retractor ultimus* (Fig. 10 B, *m.ret.ult.*) (m. radiales ventralis of Eggert) originates from the posterior rim of the dome and inserts on to the posterior border of the last, or sixth, ray. Eggert regards this muscle as an adaptation to the suctorial function of the pelvic fins. Its reduction in size in the case of *P. koelreuteri* may be correlated with the loss of suctorial function in this species.

The shift from abduction to retraction that has taken place in the action of certain muscles, largely as a result of the more lateral situation of the rays in *P. koelreuteri*, has enabled the pelvic fins to participate in terrestrial locomotion by actively contributing to the propulsive thrust. While the rays are held in a fully abducted position by the *M. abductor profundus*, the three muscles *M. retractor dorsalis*, *M. retractor ventralis* and *M. abductor medialis* will all act as powerful retractors of the rays, and thus enable the rays to be used as struts to push the fish forward. This will be clearly seen from the subsequent analysis of locomotion on land.

The caudal fin musculature of *P. koelreuteri* corresponds closely with that described by Eggert for *P. schlosseri*, and will not be considered further.

MODES OF LOCOMOTION

Swimming

The mud-skipper has two distinct modes of swimming : ' paddling ', and ' fast swimming '. The latter is to be regarded as an escape reaction, for it is only used when danger threatens and the fish is prevented from seeking refuge in its burrow. On plunging into the water the fish expels the air contained in its bucco-pharynx, and starts swimming by vigorous sinuous movements of the

tail alone. The first dorsal fin, and the two pectoral fins, remain closely folded against the body. The first four or five postaxial rays of the pectoral fins are, however, partly flexed to form horizontal hydrofoils, as shown in Fig. 11 B and D. The absence of a swim-bladder causes the fish to swim heavily across the bottom, but, after being submerged for a few minutes, it will swim to the surface, replenish the buccopharynx with air, and float comma-like at the surface.

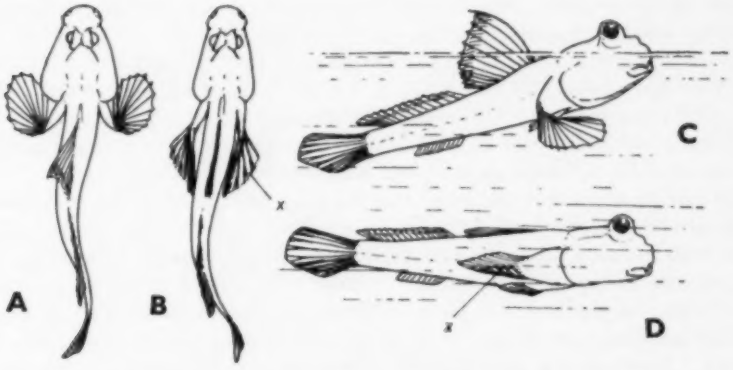


Fig. 11.—Swimming postures of *Periophthalmus* ; dorsal and lateral views. A & C paddling; B & D fast swimming. ×—Hydrofoil formed by flexion of the postaxial rays.

At other times *Periophthalmus* will paddle along slowly near the water's edge using the spread pectoral fins as paddles to supplement the swimming movements of the tail. Owing to the bouyancy of the head when the bucco-pharynx is filled with air, the fish paddles along in the peculiar posture shown in Fig. 11 C. The dorsal fins are frequently held erect during this mode of swimming, but this appears to be connected with reproductive display.

Movements on land

(1) *Ambipedal progression or crutching*

Perhaps the best analogy that can be drawn to the mud-skipper's slow, halting movements on land, is that of a cripple swinging along on a pair of crutches. The cripple swings his body forward on the crutches, and, at the end of the stroke, transfers his weight to his legs while the crutches are carried forward ready for the next cycle. In a similar manner the pectoral fins of *Periophthalmus* act as crutches to carry the body forward. At the end of the stroke the weight of the body is transferred to the pelvic fins which function in the same way as legs. It will be seen from this that the characteristic ambulatory rhythm of tetrapods, in which the limbs are moved alternately in a definite time sequence (Gray, 1953), does not occur in the case of *Periophthalmus* ; consequently the term ' walking ' cannot be applied to this animal.

One of the most striking differences between the terrestrial progression of *Periophthalmus* and the locomotory pattern of lower tetrapods is the absence

of sinuous body movements. The mud-skipper holds its body straight and quite rigid whilst moving on land. This unusual feature is intimately connected with the way in which the weight of the body is supported. In a quadruped the centre of gravity lies between the anterior and posterior limbs, but in *Periophthalmus* the centre of gravity lies behind both pairs of fins in a manner analogous to a small aeroplane of the old biplane type. The mud-skipper supports its body at three points : the two fins anteriorly, and the ventral rays of the caudal fin posteriorly. It will be noted that the tail cannot be lifted off the ground. It is forced to trail along in the mud since the centre of gravity lies between the fins and the tail skid.

Whilst crutching over the surface of the mud the tail region of the body is slightly arched so that the ventral body surface is lifted off the ground. Both Petit (1921) and Harms (1929) state that the anal fin remains in contact with the ground, but in the case of *P. koelreuteri* it has been shown experimentally that the anal fin is folded clear of the surface.

The arched posture of the body and the close proximity of the pectoral fins to the centre of gravity are adaptive in another respect. The friction of the tail fin with the mud produces a backward drag which opposes forward motion. If the pectoral fins are to push the fish forward it becomes a mechanical necessity that the grip of the fins (i.e. their friction with the ground) shall be greater than the tail drag ; for if this were not so, the forefins would merely slip over the mud. Owing to the close proximity of the centre of gravity to the pectoral girdle, the weight is very unevenly distributed between the supports. The tail is only required to carry a weight in the order of 1/10th of the total body weight. Since friction is proportional to weight, it follows that the tail drag is only a fraction of the frictional grip of the pectoral fins (assuming that the coefficient of friction for tail and fins is the same). From this it will be seen that the greater part of the propulsive force, developed in the fin muscles, is available for accelerating the fish forward, or overcoming internal resistance.

A tetrapod can lift any one of its legs off the ground without upsetting its equilibrium, provided that the centre of gravity lies within the triangle formed by the other three. Thus, by moving one limb at a time, it is possible for a quadruped to walk without at any moment upsetting its stability (Gray, 1944; Barclay, 1946). But with the three point support of *Periophthalmus* it is impossible to remove any one support without immediately upsetting the fish's equilibrium ; for this reason locomotion by the independent movement of the fins would be quite impossible. The only way in which the fish can maintain its stability is to synchronize the fin movements bilaterally, and make those of the pectoral fins alternate with the movements of the pelvic fins. This, in fact, is what the mud-skipper does. The regular sequence of fin movements is clearly indicated in the upper part of Figs. 13 and 14.

(a) The locomotory cycle

The cycle of movements made by the paired fins as the fish crutches over the mud is shown in Fig. 12. The pictures have been traced from a motion film, frame by frame, for one complete cycle.

At the commencement of the locomotory stroke the tips of the pectoral fins are lowered into contact with the ground in a forward position [frames

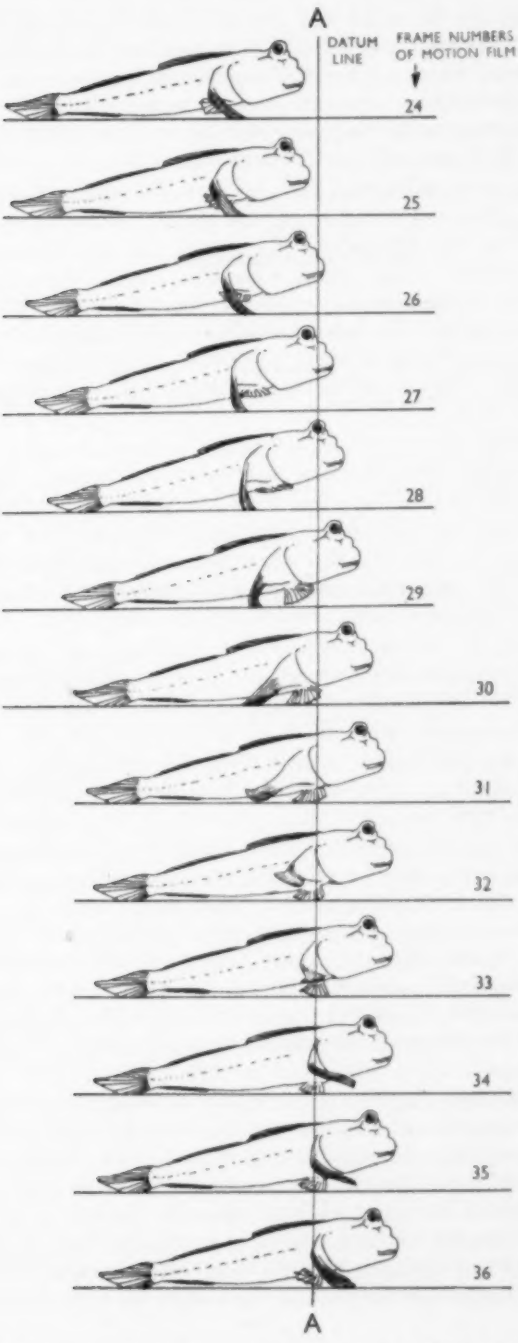


Fig. 12.—Cycle of fin movements during locomotion on land by crutching. Traced from a motion film. Each frame represents a time lapse of 0.03 secs.

35–36], possibly by the combined action of the *M. depressor radiorum* and *M. levator superficialis*. The basal lobe at this instant is fully abducted and the rays of the fin, which are bundled together to form a strut, are held almost parallel to the body axis. In the case of *P. koelreuteri*, the fin is never spread while the fish is moving on land, although Eggert states that this does happen in the case of *P. chrysospilos* and *P. argentilineatus*.

The propulsive stroke of the pectoral fin is a complex action. Essentially it involves an adduction of the basal lobe and an extension of the fin, but, as the fin rays are held in a depressed position by the *M. depressor radiorum* and *M. flexor superficialis*, the extensor complex causes the postaxial rays to swing in a vertical plane, analogous to the pole of a punt. Consequently the fish is lifted and carried forward on its pectoral fins [frames 24–28]. The stress set up at the shoulder joint is taken by the *M. coraco-radialis*, which virtually carries the weight of the body. This muscle will also contribute to the adduction of the basal lobe.

While the fish is moving forward on its pectoral fins, the pelvic fins are raised and brought forward ready for their next cycle. The whole pelvic girdle is lifted off the ground by the *M. levator pelvis*, and at the same time the rays are adducted [24]. The rays are protracted to a forward position [27–28], and then abducted [29]. Finally, the whole pelvic girdle is lowered by the *M. protractor pelvis* in such a way that the posterior rays touch the ground a fraction of a second before the pectoral fins are lifted [30].

At the beginning of the recovery stroke the pectoral fin is lifted off the ground by the *M. levator superficialis* and *M. interradii* [30–31]. The fin rays are now flexed by the two flexor muscles and the *M. depressor radiorum* until the fin has been moved through an angle of about 90° [32]. At this point abduction of the basal lobe starts. Simultaneous flexion and abduction continue until the rays have been brought almost parallel to the body axis, but slightly declined to it [34].

During the recovery stroke of the pectoral fins, the weight of the body is taken by the pelvic fins. At first only the posterior rays take the weight [31], but as the fish continues to move forward, partly under its own momentum and partly by the activity of the pelvic fin muscles, it rolls on to the anterior rays [32–34]. By the time the pectoral fins have been brought forward, the fish is mainly supported on the anterior rays of the pelvic fins, and the posterior rays are beginning to lift off the ground [35]. As the weight is finally taken by the pectoral fins, the remainder of the pelvic rays are retracted and adducted [36–24].

It will be realized that the crutching of *Periophthalmus* differs from the movements of seals, to which the fish has been likened (Pellegrin, 1923). For, although the pectoral 'flippers' of the Southern Elephant seal—*Mirounga*, and young Grey seals—*Halichoerus*, are moved forward together (Matthews, 1929 ; Davies, 1948), it would appear that the main propulsive force is generated by the lumbar muscles, which hitch the pelvic region forward and then thrust the chest forward by straightening the back. The pectoral limbs presumably do not propel, but rather lift the body to reduce friction with the ground.

(b) Analysis of motion

In Fig. 12 the positions of the fins during the locomotory cycle have been traced from a motion film. The vertical datum line A—A marks a fixed point on the ground, and the interval between successive pictures represents a time lapse of 0.03 secs. It will be seen in this particular instance the complete cycle took 0.4 sec. during which time the fish moved forward 4·3 cm. In round figures this gives a speed of about 10 cm/sec. for a fully grown fish 14 cm. long.

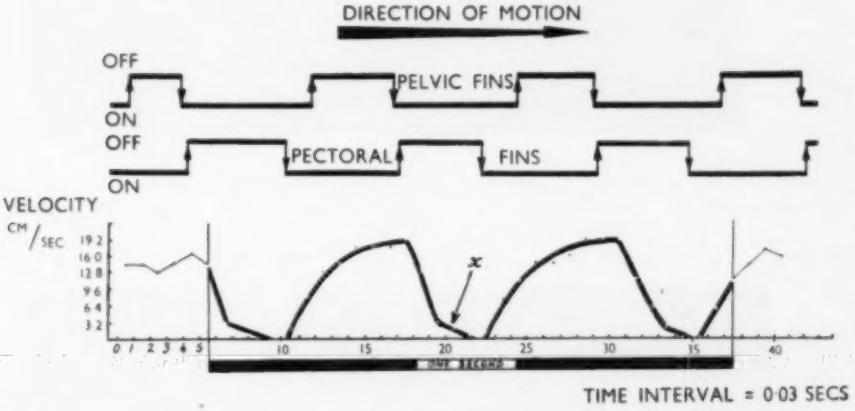


Fig. 13.—Analysis of crutching on land. Upper Fig. shows alternation of pectoral and pelvic fin movements with respect to time. Lower Fig., velocity curve for two consecutive cycles. ×—pelvic thrust (see text).

By plotting distance travelled between successive frames against time, a velocity curve was constructed for a period extending a little over one second (Fig. 13). It covers two complete locomotory cycles. The curve shows that there is a very rapid acceleration at the commencement of the propulsive stroke. The acceleration gradually falls off as the fish gets under way, until an almost uniform velocity of about 19 cm./sec. is reached. At the instant the pectoral fins lift, there is a very rapid, and apparently uniform, deceleration which is partly due to the braking action of the pelvic fins.

Inger (1952), by his statement that the pelvic fins " . . . do not propel the body as readily ", implies that the pelvic fins do contribute to propulsion, although he does not state on what evidence this conclusion is based. From the tracings of the motion film (Fig. 12) it can be seen that the fish does continue to move forward after the pectoral fins have been lifted. It is impossible, however, to decide by mere inspection whether this movement is due to the momentum acquired during the propulsive stroke, or whether the pelvic fins are playing an active role in propulsion. From the relationship between distance and time shown in Fig. 14, it will be seen that during each cycle the fish travels about one-third of the total distance while the pectoral fins are off the ground. This, together with the fact that the pelvic musculature exerts a powerful retraction of the rays when held in the abducted position, strongly

suggests that the pelvic fins do take an active part in terrestrial progression. Positive evidence has, however, been obtained from a closer study of the velocity/time curve (Fig. 13).

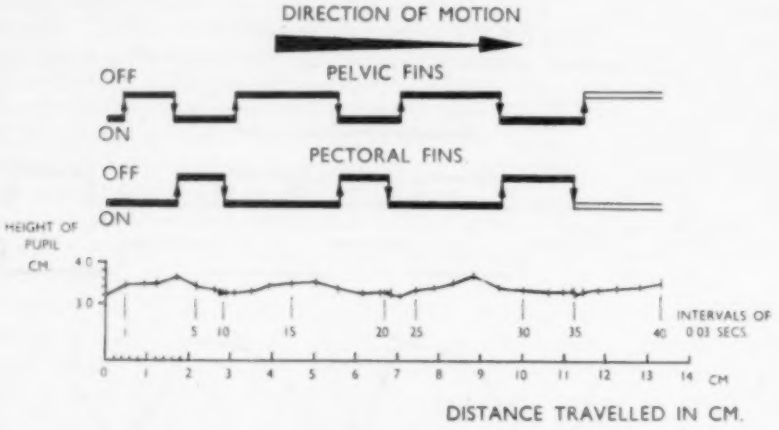


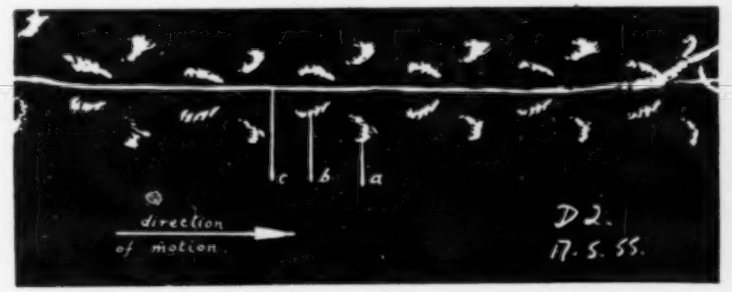
Fig. 14.—Analysis of crutching on land. Upper Fig., shows alternation of pectoral and pelvic fin movements with respect to distance travelled. Lower Fig., locus of a point (the pupil of the eye). Time intervals of 0.03 sec. duration are indicated by vertical lines on the curve.

It has already been noted that the velocity falls off rapidly as soon as the pectoral fins are lifted, but before actually coming to a halt, there is a sudden change in deceleration which produces the curious tail to the velocity curve (Fig. 13, ×). This change in acceleration can only be interpreted in one way. Initially the pelvic fins exert a braking action, possibly by merely increasing friction with the ground, which causes the rapid drop in velocity. By the time the fish has reduced its velocity to about 3 cm/sec. the pelvic fins are exerting a forward thrust on the body. This thrust is not sufficient to cause acceleration, but it does check the rapid drop in velocity, which now falls off at a lower rate. If the pelvic fins did not exert a propulsive force this tail would be absent from the curve.

Lastly, it may be noted that the velocity falls to zero at the end of the recovery phase. This normally lasts about 1/20th of a second when followed immediately by another cycle, but it can be prolonged to a resting period of indefinite length.

The locomotory cycle can be divided into periods when the fins are ' on ' and ' off ' the ground. These periods have a definite relationship with each other in the sequence of movements, and have been represented diagrammatically in the upper part of Figs. 13 and 14. Both pectoral and pelvic fins stay ' on ' the ground for approximately 0.25 sec., and ' off ' for another 0.15 sec. making a total duration of 0.4 sec. for the complete cycle (Fig. 13). The sequence of ' on ' and ' off ' movements for pectoral and pelvic fins is approximately 90°

out of phase, although it will be noted that the lifting of the pelvic fins lags behind the pectoral fins by a slightly longer period than the reverse process.



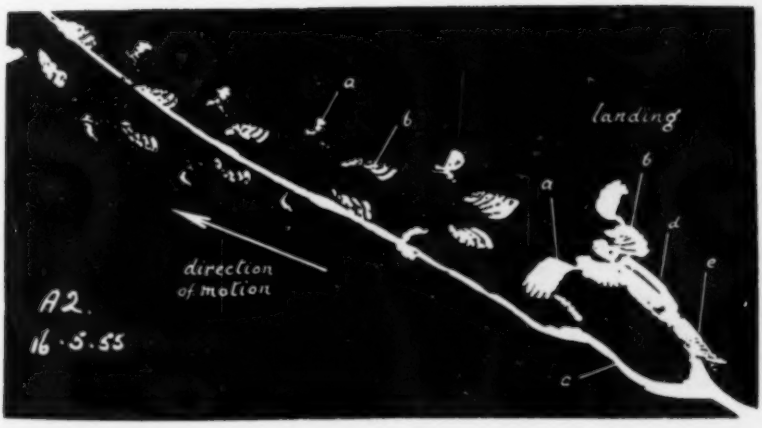


Fig. 15.—Autographic records made by *Periophthalmus* crutching across a piece of glass covered with soot.

a. trace of pectoral fin ; b. trace of pelvic fin ; c. trace of caudal fin ; d. impression of ventral part of body ; e. trace of anal fin.

(c) Autographic records

By allowing the fish to move about on a piece of glass covered with a thin film of soot, a record was obtained of those parts of the fish that made contact with the glass. These records have proved useful in interpreting certain points that could not be determined photographically.

Two typical autographic records are shown in Fig. 15 A and B. Both show the very regular impressions made by the pectoral and pelvic fins, and the straight trace left by the ventral rays of the caudal fin. These traces bring out very clearly the fact that the body does not make any sinuous movements

while the fish crutches on land, although it may happen that the tail trace lies a little to one side if the tail happens to be bent in that direction (Fig. 15 B). This appears to be in contradiction to the findings of Martens (1881), who gives a woodcut showing a sinuous tail trace. His figure is in error, however, since it omits to show the impressions made by the pelvic fins.

It can be seen from the autographic records that the fish moves along on the tips of the fin rays only. There is no twisting of the fin rays relative to the ground as suggested by Eggert (1929) for *P. schlosseri*, nor are the rays spread while on land. It is probable that, since *P. schlosseri* cannot bunch up its rays or pull them in towards the body as effectively as *P. koelreuteri*, its pectoral fin rays tend to describe an arc more or less in the horizontal plane, and not swing in the pendulum-like manner of *P. koelreuteri*.

(ii) *Skipping on land*

Skipping appears to be an escape reaction used by the fish to reach the safety of water, or its burrow, as quickly as possible. Occasionally the skip is used in feeding, or at the commencement of climbing. Superficially the skip resembles the tetrapod ' jump ', but it differs from this activity in so far that it is the tail and not the hind limbs which project the fish into the air.

At the beginning of the skip the tail is turned to one side, and the stiff ventral rays of the caudal fin depressed into the mud. It is possible that the short stiff rays of the anal fin are likewise depressed. This anchors the hind end of the body and provides a fulcrum against which the axial muscles can push, then, by a sudden and powerful straightening of the tail, the fish is projected into the air. This tail thrust will only act in the horizontal plane, i e., it will push the fish forward, but it is clear from observation of the skip that the fish actually leaves the ground, and may rise 2 to 3 cm. There must, therefore, be a vertical component to the force propelling the fish. The lifting force acting vertically upwards appears to be supplied mainly, if not entirely, by the pelvic fins. The anterior end of the fish is accelerated upwards by a sudden contraction of the *M. depressor pelvis* and anterior hypaxial bundle, at precisely the same instant that the forward thrust is given by the tail. The resultant of these two forces determines the trajectory of the fish.

The extent to which the pectoral fins play an active role in skipping is uncertain for the fish is still able to skip when they are bound to the sides, although when this is done the fish is unable to balance properly. Petit (1921) believed that the pectoral fins actively helped the tail in the skip, and he noticed that young mud-skippers could move by short bounds from one stone to another without the aid of the tail. A similar phenomenon has been noticed in the present study with fish about 2 cm. long, but here it is considered that the propulsive force comes from the pelvic fins rather than the pectoral fins. If this interpretation is correct this activity of the young fish becomes a true jump.

The impact on landing is taken by the pelvic fins and the ventral part of the tail (Fig. 15 B). The pectoral fins are spread prior to landing, and probably act as props which prevent the fish toppling over sideways.

A fully grown mud-skipper (14 cm. long) can cover distances of 30 to 40 cm., i.e., up to three times the body length, in a single skip.

(iii) *Climbing*

Mud-skippers are able to climb to a limited extent, and are often found clinging to the prop-roots of the mangrove trees just above the water. They climb out on to the more horizontal roots by means of their paired fins, just as if they were on land. At other times they will skip out of the water and adhere to the vertical prop-roots, but beyond this activity the fish do not seem to be able to climb any higher. The climbing ability of *P. koelreuteri* is inferior to that of other species of *Periophthalmus* due to the modified nature of the pelvic fins.

As already shown above, the pelvic fin rays are short and stiff, and the two fins remain separate structures. This is clearly an adaptation to crutching and skipping on land, and is in sharp contrast to species, such as *P. schlosseri* or *P. chrysospilos*, which have longer and more flexible rays, and in which the fins are joined together by a web of skin at both front and back to form a sucker. The mechanism by which the pelvic fins exert their suctorial action in *Gobius caninus* and *P. schlosseri*, has been described by Eggert (1929). The suctorial nature of the pelvic fins of *P. chrysospilos* is clearly seen from the photograph given by Eggert (1929 b).

Skimming on the water

The mud-skipper can skim across the water in a series of bounds. This is a very rapid mode of progression, and, like the skip, appears to be a flight reaction to danger. Petit (1921) noted that each bound is preceded by a short period of swimming. It is during this very short period in the water that the propulsive forces for the bound through the air are generated. The view held by Inger (1952) that skimming is a series of skips on the water's surface is quite erroneous : skipping and skimming are, from a locomotory point of view, quite dissimilar. Each bound is a deliberate and strenuous act on the part of the fish to throw itself out of the water, and is not a passive rebound like that made by a missile. For this reason the term ' ricochet ' frequently used by French authors seem inappropriate.

Skimming has been studied by means of motion pictures taken under natural conditions in the fish's habitat. Although the absence of fixed points in the pictures preclude accurate determination of velocity and acceleration, some useful information has been obtained from the films.

In one series of pictures it was possible to estimate the distance traversed in two consecutive bounds, and this gave a speed of just over 2·5 metres/sec., for a fish approximately 14 cm. in length. This value seems considerably lower than the velocity quoted by Gray (1953) for the flying fish *Exocoetus*, although it must be realized that the above value for *Periophthalmus* includes the period of acceleration and landing in the water, as well as the actual flight through the air. The motion pictures clearly show that the impetus necessary to project the fish out of the water is generated by vigorous swimming movements of the tail alone, and in this respect *Periophthalmus* closely resembles *Exocoetus*.

Each bound can be divided into three phases :

(a) an active swimming phase during which the momentum necessary to carry the fish through the air is generated (Fig. 16, a–b–c) ;

(b) projection through the air (Fig. 16, d–e) ;

(c) landing on the water's surface (Fig. 16, f–g–h). Starting from the normal swimming position with its eyes and part of the head out of the water, the fish folds back its pectoral fins and starts to swim rapidly. This causes the anterior part of the fish to be thrown out of the water at an angle of 30° to the horizontal (Fig. 16), in the following way. The tail, second dorsal and

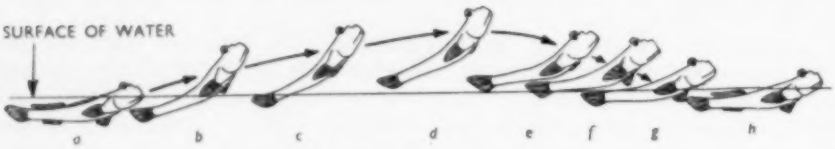


Fig. 16.—Skimming on water. a–h A single bound ; redrawn from motion film. Note : in this Fig. time intervals between consecutive positions of the fish are not of equal duration.

anal fins produce a forward thrust by sinuous movements of the body, but the caudal fin imparts a downthrust to the posterior part of the body, owing to its stiff truncated lower lobe. At the front end of the body, anterior to the centre of gravity, the pelvic fins and the bouyancy of the head produce a lifting force. This anterior lifting force, and the posterior downthrust, form a couple which lifts the anterior end of the fish out of the water. The fish continues to swim vigorously as the rest of the body emerges ; the tail thrashes the water until it is lifted clear of the surface. The fish now travels through the air with the pectoral fins folded to the sides. The flight does not last long, usually in the order of 1/20th of a second, during which time a distance of 20 to 40 cm. is traversed.

The ventral side of the tail and the caudal fin are the first parts of the body to touch the water, and they are immediately followed by the rest of the body. As the fish sinks into the water the vigorous swimming movements are again commenced in preparation for the next bound. The pectoral fins are not used to prevent the fish sinking, as believed by Eggert (1929), but are folded to the sides. The pelvic fins, however, appear to be spread fan-wise when landing, and may well serve to break the impact of landing on the surface.

DISCUSSION

Consideration of the anatomy and locomotion of *Periophthalmus* might be expected to throw some light on the way tetrapod ancestors modified their fins and locomotory pattern for life on land. But a closer investigation shows that, apart from the fact that both the mud-skippers and the lower tetrapods use their paired appendages for movement on land, all further analogy between the two groups breaks down.

The most important single influence contributing to this divergence of locomotory mechanism was the ancestral position of the paired fins. The

lower tetrapods inherited from their crossopterygian ancestors a posteriorly situated pelvic girdle, which resulted in a wide spacing of the limbs. This feature was probably a great advantage in the early evolution of the locomotory pattern, as it provided a ' lever arm ' at either end of the body by means of which the sinuous swimming movements could be translated into a propulsive thrust parallel to the body axis. At a later date in tetrapod history this feature made it possible for the limbs to take on the role of supporting structures which could carry the body clear of the ground, and thus reduce frictional forces. The musculature of the limbs, and not the axial musculature, then became the primary source of the propulsive force.

On the other hand, the anterior location of the pelvic fins in *Periophthalmus*, and the rest of the Gobiidae, makes it impossible for their fins to assist sinuous swimming movements in pushing the fish forward. Moreover, since both pectoral and pelvic fins are anterior to the centre of gravity, they cannot alone support the body off the ground ; as a result the caudal fin is utilized to support the posterior end of the body. It will also be noted that the struts used to lever the fish forward are formed from the dermal fin rays, whereas in tetrapods it is the endoskeletal structures of the limb that are involved.

In consequence of these structural peculiarities, the neural mechanisms that gave rise to the ambulatory pattern of tetrapods would be quite ineffective in the case of *Periophthalmus*. Presumably a different type of neural locomotory mechanism, producing a bilateral synchronization of fin movements instead of the diagonal co-ordination exhibited by tetrapods, was developed by certain teleosts in response to the need for more delicate control of movements, such as ' braking ', whilst swimming. Such neural mechanisms have been taken over directly by *Periophthalmus* for co-ordination of its ambipedal pattern of locomotion.

There are certain features of a specialized nature in the structure of *Periophthalmus* for which there are no strict parallels among tetrapods. For example, the mud-skipper has not succeeded in converting the shoulder joint into a bearing surface comparable to the glenoid, but it has overcome this difficulty by modifying the coraco-radial muscle so that it takes the weight of the body at the joint. The close proximity of the pelvic and pectoral girdles has made it possible for these two structures to articulate. From this articulation *Periophthalmus* has developed its highly adaptive pelvic suspension ; a mechanism not only allowing the body weight to be transmitted to the pelvic fins, but also providing a mechanism for the production of a lifting force which is used in skipping.

SUMMARY

1. The following structural modifications of *Periophthalmus koelreuteri* (Gobiidae) are of particular importance in locomotion on land.

(a) A strengthening of the pectoral girdle by increased ossification, and an enlargement of the areas for muscle attachment. The postaxial rays of the fin are stiffened considerably, and are of the semi-spinous type. No fusion of the radial elements occurs in this species.

(b) The relative extension and depression of the pectoral fin axis is greater

for *P. koelreuteri* than other species. This enables the postaxial rays to be swung in almost a vertical plane. The pectoral fin rays are not spread in this species when moving on land, but are bundled together to form a strut.

(c) In addition to adducting the basal lobe, the *M. coraco-radialis* takes on the new role of maintaining the stability of the shoulder joint, and supporting the body weight.

(d) The pelvic bones articulate with the cleithrum, and act as compression struts transmitting the body weight to the pelvic fins. The *M. protractor pelvis* and the anterior hypaxial musculature play an important part in supporting the body, and in providing the vertical component of the forces used in skipping. The pelvic fin rays are short and stiff. The first is spinous and the remainder semi-spinous. The pelvic fins are modified for support, and have lost their suctorial ability.

(e) The caudal fin is truncated ventrally. The short stiff ventral rays are used to anchor the tail during the skip, and to support the hind end of the body when moving on land.

2. Six modes of locomotion are defined and analysed.

(a) *Fast swimming* is effected by the tail without the assistance of the paired fins.

(b) *Paddling* is a slow mode of swimming in which the pectoral fins are used as paddles. Air in the bucco-pharynx causes the fish to swim with the head partly out of the water.

(c) *Crutching* is a slow halting motion on land in which the fish is hitched forward on the pectoral fins. The trunk and tail remain stiff, and do not make any sinuous movements. The caudal fin acts as a skid to support the hind end of the body off the ground. A bilateral synchronization of the paired fins is necessitated by the instability of a three point supporting system. Motion is discontinuous, i.e., it comes to a momentary halt at the end of each locomotory cycle. Analysis of motion films has given conclusive evidence that the pelvic fins contribute to the propulsive thrust, but their contribution is very small. A speed of about 10 cm/sec. is achieved by adult fish (*c.* 14 cm. body length).

(d) In *skipping* the fish is projected through the air by a propulsive force developed in the axial muscles of the tail. A vertical component is produced by the *M. protractor pelvis* and the hypaxial muscles. The caudal fin acts as a fulcrum for the skip.

(e) *Climbing.* The ability of *P. koelreuteri* to climb is limited, due to the fact that the pelvic fins have been modified for a locomotory, rather than a suctorial, function.

(f) *Skimming* is an activity in which the fish makes a series of bounds over the water. The momentum for each bound is generated by vigorous swimming movements of the tail. A speed of about 2·5 metres/sec. is achieved. Skimming is an escape reaction.

3. The adaptations shown by *Periophthalmus* and tetrapods to terrestrial progression are constrasted, and its bearing on the evolution of the two groups from aquatic ancestors is discussed.

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THE SPAWNING OF *ARENICOLA MARINA* (L.) IN THE BRITISH ISLES

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(With 4 figures in the text)

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INTRODUCTION

Published accounts of the breeding of *Arenicola marina* (L.) show that striking differences in the time of spawning may occur (Storrow, 1925 ; Newell, 1948 ; Smidt, 1951). The work reported here was undertaken to throw further light on this problem. It includes (a) an intensive study, lasting for a year (1950–51), of the lugworms on two beaches in the Isle of Man, and (b) observations on worms from a number of other British localities, made during the breeding period of 1951.

SPAWNING IN THE ISLE OF MAN

The two populations studied in detail came from different types of beaches in the Isle of Man ; one lived in a sheltered inner harbour at Port St Mary, where the deposit was dark muddy sand, and the other in a small sandy beach called Strandhall which was considerably exposed to wave action generated by the prevailing south-westerly winds (Fig. 1).

Methods

The populations were sampled at a series of stations set at about 50 feet apart and extending from high water to low water marks. One square metre of soil, from which all lugworms were removed, was sampled from each station at monthly intervals. At Port St Mary, the monthly samples varied between 149 and 336 worms, and at Strandhall between 63 and 272 worms ; in all, over three thousand worms were collected from the former beach and over

two thousand from the latter. During November 1950 the routine sampling was stopped to study the spawning of the population ; special spawning samples of between 40 to 100 worms were collected at weekly intervals from between mid tide level and low water neaps (the region occupied by adult worms un-

Fig. 1.—Maps of the British Isles and the south of the Isle of Man.

covered during neap tides and accessible during both spring and neap tides).

From each undamaged worm from Port St Mary and Strandhall the following information was obtained ; its size as volume in c.c., its state of sexual

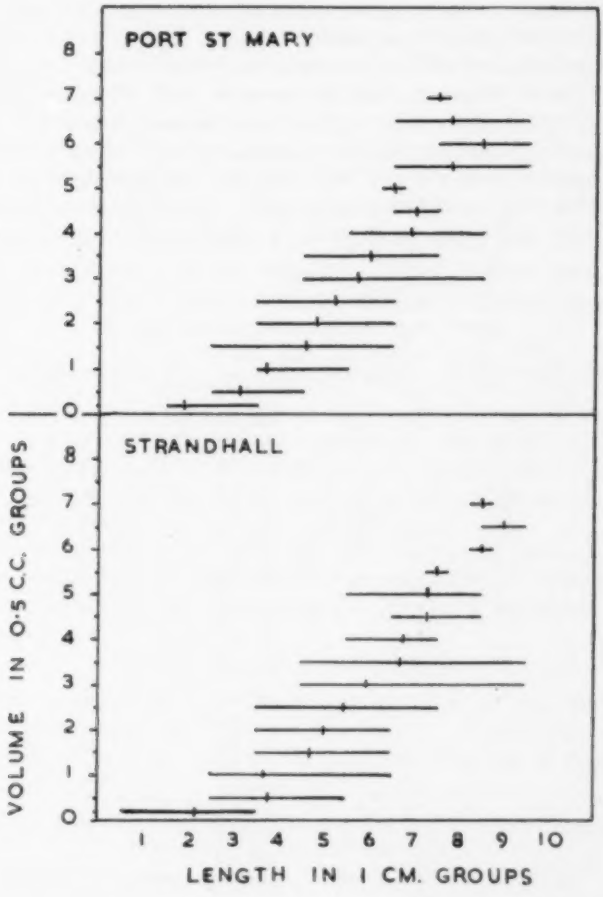

Fig. 2.—The range of lengths of the anterior chaetigerous region of the body found within each 0·5 c.c. volume group of *Arenicola marina* from Port St Mary and Strandhall.

maturity and the diameter in μ of the largest germ cell visible in the coelomic fluid.

After considering the relative merits of volume, length and weight as criteria of size in *Arenicola marina*, it was decided to use volume and length. Length is the more generally accepted measure of size, and Newell (1948) has used it successfully by taking the length of the chaetigerous region of freshly dug worms in a state of moderate contraction which they assume after handling. The Whitstable worms however were considerably larger than those from

the Isle of Man and it is clear from Fig. 2 that for populations of small worms, length is a crude measurement of size. Volume is a more refined criterion since it is possible consistently to measure adult worms down to 0·3 c.c. and juvenile worms to 0·01 c.c.; moreover it is easy to measure even the smallest of worms. Volume however has the disadvantage of including the frequently damaged tail region, which is avoided in length. Weight was rejected because it was likely to be a misleading criterion in an animal which may contain sand or mud of variable weight in variable amounts. Table 1 gives the percentage frequency of length and volume groups from Strandhall and Port St Mary.

All the lugworms were sexed by examining the coelomic fluid for developing germ cells because these are released from the very small gonads at an early stage. Worms with no coelomic germ cells were either juveniles or sexually inactive adults and these could only be distinguished by their size. The

TABLE 1

The percentage frequency of length and volume groups of *Arenicola marina* collected from Port St Mary and Strandhall between 1950–51.

Length in cms.	Port St Mary	Strandhall	Volume in c.c.	Port St Mary	Strandhall
less than 0·9	×	1	less than 0·5	7	32
1·0–1·9	3	12	0·5–0·9	8	26
2·0–2·9	8	35	1·0–1·4	14	14
3·0–3·9	27	23	1·5–1·9	16	9
4·0–4·9	31	14	2·0–2·4	14	5
5·0–5·9	18	8	2·5–2·9	9	4
6·0–6·9	8	4	3·0–3·4	5	3
7·0–7·9	3	1	3·5–3·9	3	3
8·0–8·9	1	1	4·0–4·4	2	1
9·0–9·9	×	×	4·5–4·9	1	1
10·0–10·9	×	—	5·0–5·4	1	1
			5·5–5·9	×	×
			6·0–6·4	×	×
			6·5–6·9	×	×
			7·0–7·4	×	×
			7·5–7·9	×	—
			8·0–8·4	×	×
			8·5–8·9	—	—
			9·0–9·4	×	×
			9·5–9·9	×	—
			10·0–10·4	—	×
Arithmetic mean	4.5 cms.	3·4 cms.		2·0 c.c.	1·2 c.c.
Numbers of worms	2350	1408		2915	1737

(× represents less than 1 per cent.)

concentration of the genital products in the coelom changes throughout the year. Using the concentration, appearance and size of coelomic germ cells, the state of sexual development of each individual was assessed, and the worm was placed in one of the following arbitrary categories :

Unripe : These are worms containing germ cells of varying sizes, but mostly small, and in low concentration, but in sufficient numbers to colour the coelomic

fluid slightly. The oocytes have little or no yolk ; the sperm plates are pale with no tails and consist of spermatogonia, spermatocytes or spermatids.

Ripe : These are worms containing maturing germ cells of medium or large sizes, which tend to fill the coelomic cavity. The coelomic contents appear white in the male and orange in the female and such worms are usually called ' milky '. The oocytes vary between 150 μ and 170 μ and are full of orange yolky cytoplasm ; the sperm plates are mostly discs of tailed spermatozoa, and just prior to spawning the worms are turgid.

Spawning : These are worms which contain large, apparently mature germ cells, but rather fewer than in the previous category, because some have already been released. Although the coelomic fluid is still coloured white or orange, it is more liquid in consistency, and the worms are no longer turgid.

Spent : These are worms with only a few large apparently mature germ cells, and the coelomic contents appear colourless. These worms have completed their spawning, and so their presence is a useful indication of the occurrence of spawning.

Empty : These are worms with no coelomic germ cells. They include both ripe worms which have spawned completely and juveniles which are not yet sexually developed. The composition of the ' empty ' group therefore varies throughout the year and just prior to spawning it consists mostly of juvenile worms. Since the proportion of juvenile worms varied greatly in different populations, all the spawning dates refer to samples from which juveniles, distinguishable by their size, have been removed.

The time of spawning was determined by observing where possible the appearance of sperm puddles (egg puddles were only rarely seen) on the surface of the sand or by examining the coelomic contents of preserved worms as described above.

Size and age of sexual maturity.

Table 2 shows the percentage of worms in each 0·5 c.c. size groups which were sexually mature just before the breeding season. The figures suggest that lugworms are capable of breeding for the first time at a size of about 0·5 c.c.

TABLE 2

The percentage number of sexually mature worms in each 0·5 c.c. size group during October 1950 at Port St Mary and Strandhall.

Size Group (in groups of 0·5 c.c.)	Port St Mary	Strandhall
	Percentage	
Less than 0·5 c.c.	0	5
0·5–0·9 c.c.	40	25
1·0–1·4 c.c.	73	33
1·5–1·9 c.c.	91	57
2·0–2·4 c.c.	83	66
2·5–2·9 c.c.	100	100
3·0–3·4 c.c.	85	100
3·5–10·4 c.c.	100	100

The determination of the age at which sexual maturity is attained is more difficult because we do not know how to age lugworms. Fortunately, in 1950, a considerable number of these very young worms settled in nursery

patches which were slightly isolated from the rest of the population at both shores. It was therefore possible to sample them separately at regular intervals and so determine their growth rate. It was found that the worms ranging from 0·14 c.c. to 0·5 c.c. were nineteen months old at Port St Mary and twenty-two months old at Strandhall. Several attempts to keep some of these very young worms alive in laboratory tanks proved unsuccessful, although one worm out of an original forty did survive for over two years ; when twenty-seven months old it had attained a size of 0·49 c.c.

It seems reasonable to suggest that those worms between 0·5 c.c. and 0·9 c.c. which were sexually mature in October 1951 (see Table 2) were probably two years old. This agrees with Newell's (1948) and Smidt's (1951) statements that *Arenicola marina* spawns for the first time in its second year of life. Many worms however are a little larger (and possibly older) than this before they become sexually mature and spawn for the first time.

Spawning at Port St Mary

Fig. 3 shows a very rapid decline in the percentage of worms with coelomic

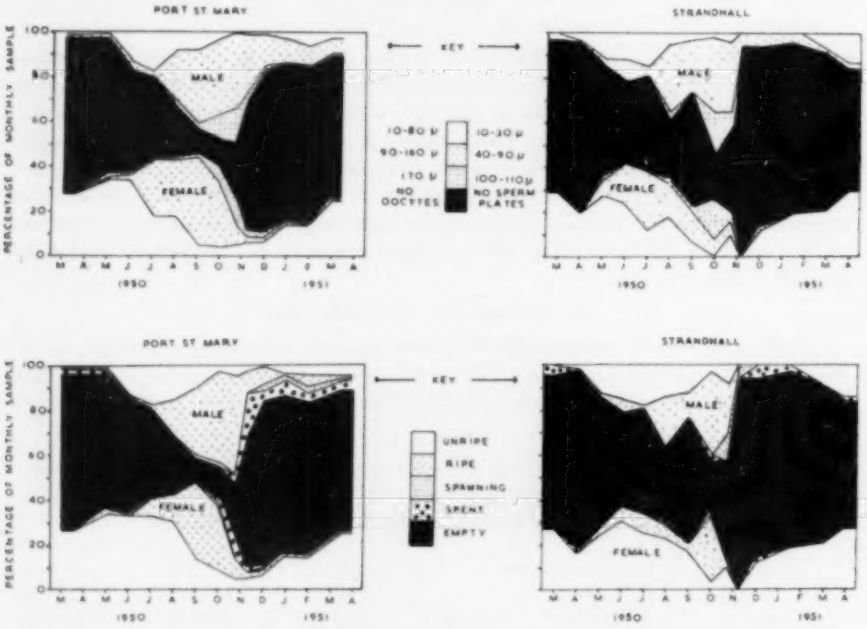

Fig. 3.—The sexual development of *Arenicola marina* throughout one year at Port St Mary and Strandhall (juvenile worms have been excluded). The upper two graphs show the changes in the proportions of male and female worms with different sizes of coelomic germ cells. The lower two graphs show the changes in the proportions of male and female worms at different stages of sexual maturity.

germ cells during November and indicates that spawning occurred during that month, although female spawning possibly began slightly earlier in October.

Various other observable changes also occurred. The coelomic germ cells reached their maximum size in November. The very great decrease in mean size of coelomic oocytes after November (from 14·4 μ in early November to 9·3 μ in late November) indicates the loss of the large oocytes during spawn-

TABLE 3

Changes in the sexual condition of *Arenicola marina* at Port St Mary during the breeding seasons of 1950 and 1951 (the figures are percentages of samples).

	PORT ST MARY 1950							
State of sexual maturity	Oct. 4th	Oct. 11th	Oct. 20th	Oct. 28th	Nov. 4th	Nov. 10th	Nov. 17th	Nov. 24th
Unripe males	1	1	3	—	1	—	3	—
Ripe males	30	32	35	41	42	10	4	14
Spawning males	2	3	9	2	1	—	3	2
Spent males	—	1	3	—	5	22	18	17
Unripe females	6	7	1	2	3	—	9	4
Ripe females	28	33	11	33	8	5	—	4
Spawning females	8	3	15	7	1	—	—	—
Spent females	4	5	—	—	8	5	—	2
Empty worms	20	15	23	16	28	58	63	55
Total numbers of worms	72	98	88	105	61	38	44	42

	PORT ST MARY 1951			
	Nov. 12th	Nov. 17th	Nov. 22nd	Nov. 26th
Unripe males	—	—	—	—
Ripe males	40	27	5	—
Spawning males	15	15	5	—
Spent males	15	12	25	7
Unripe females	—	4	—	—
Ripe females	20	—	—	—
Spawning females	5	—	—	—
Spent females	—	12	—	—
Empty worms	5	31	65	85
Total numbers of worms	20	26	20	26

ing ; no such similar decrease occurred in the sizes of the coelomic sperm plates because not all the large ripe sperm plates were voided during spawning, and males with a few ripe sperm plates were often found during the following winter months. Female worms seem more capable of complete extrusion of their germ cells, probably because oocytes are bulkier than sperm discs.

The size of the largest germ cells found in individual worms varied considerably in any one monthly sample and also from one month to the next, as can be seen in Fig. 3. The gonads were most active during the spring, releasing very small oocytes or sperm discs into the coelom ; during the summer months, the germ cells grew larger and the oocytes attained their maximum size at 170 μ in October and November. Only a few females, however, had oocytes

of this size (8 per cent and 12 per cent of the samples respectively) because soon after reaching this size, they were spawned. There was no critical size at which the male germ cells were spawned, but during their development there were visible indications of their maturation. The disc of round rather pale spermatids developed into a darker plate of tailed spermatozoa. The percentage of worms with tailed sperm plates increased greatly from September (12 per cent of the sample) to early November (44 per cent) and dropped suddenly during November (27 per cent of the late November samples and 10 per cent of the December sample), indicating the occurrence of spawning.

It is interesting that the development of the male worms has appeared to lag slightly behind that of the females throughout the year (Fig. 3). The testes began to proliferate small sperm plates in June whereas the ovaries were active in March. It was not until November that the greatest percentage of ripe males were found, which is a month later than the peak month for ripe females. The details of the samples taken during the spawning season show that there was a difference in time of spawning of the sexes. Table 3 shows that in 1950 male spawning occurred between the samples of 4th November and 17th November whereas there was a decline in the percentage of ripe female worms from 28th October to 4th and 10th November. That is, in 1950, the female worms both began and finished spawning several days earlier than the male worms. However, in 1951, the male worms spawned between 12th and 22nd November and the female worms between 12th and 17th November, that is beginning at the same time as the males, but finishing a few days

TABLE 4

The dates of male spawning in 1950 and 1951 and the approximate numbers of sperm puddles observed on the shore at Port St Mary.

Days in November 1950	Number of Puddles in 1950	Days in November 1951	Number of Puddles in 1951
Nov. 3rd	19	Nov. 18th	56
Nov. 4th	10	Nov. 19th	989
Nov. 5th	4	Nov. 20th	285
Nov. 7th	8	Nov. 21st	235
Nov. 14th	511	Nov. 22nd	30
Nov. 15th	100	Nov. 23rd	2
Nov. 16th	582		
Nov. 17th	2		

TABLE 5

The degree of male spawning at different tidal zones at Port St Mary during the spawning periods of 1950 and 1951.

Height in feet below Ordnance Datum (=M.S.L.)	Tidal Level	Spawning Period 1950	Spawning Period 1951
		Percentage	
0·0 to −1·0	M.S.L.	5·6	2·7
−1·0 to −2·0		23·2	23·6
−2·0 to −3·0		57·5	50·6
−3·0 to −4·0	M.L.W.N.	13·5	21·2
−below −4·0		submerged	1·8
Total number of sperm puddles		1235	1597

earlier. Such a discrepancy in the times of the 1950 male and female spawning implies that the factors inducing spawning differ in the two sexes and that in 1950 these factors did not coincide.

An attempt was made to determine the precise dates of spawning by observing the actual process on the beach during the low water period. The surfaces of several beaches in the Isle of Man were searched but only at Port St Mary was any spawning seen, and that was male only. Table 4 shows that male seminal fluid was released over a period of fourteen days in 1950 and six days in 1951. However, during both seasons most of the spawning occurred during three peak days as can be seen from the counts made. Table 5 shows both that the concentration of these puddles varied at different tidal levels

TABLE 6

The proportion (and number) of ripe, spawning and spent lugworms present at Port St Mary during non-breeding months.

	Months	Male Worms				Female Worms			
		Ripe and Spawning		Spent		Ripe and Spawning		Spent	
		%	No.	%	No.	%	No.	%	No.
1950	March/April	2	(3)	2	(4)	—		—	
	May	½	(1)	2	(3)	2	(5)	—	
	—	—		—		—		—	
	December	11	(18)	4	(6)	3	(4)	2	(3)
1951	January	3	(7)	6	(14)	2	(3)	—	
	February	7	(16)	4	(9)	½	(1)	—	
	March	2	(4)	5	(14)	½	(1)	—	

and that in both years the greatest concentration was found between mean sea level and low water neaps, where the adult worms are most dense.

Clearly at Port St Mary the main spawning occurred only once during the year, in the autumn. However, in view of Fauvel's (1899) and Ashworth's (1904) statements that *Arenicola marina* has a second breeding period in the spring, it was worth examining those ripe worms found during the winter and spring. As Table 6 shows the numbers of ripe and/or spent worms were too few to consider that they indicate a second breeding period, especially as there were few females. Such ripe and spent males found out of season are probably remnants from the previous year's spawning, which failed for some reason to spawn at the correct season.

Spawning at Strandhall

The lugworms at Strandhall were investigated in the same way and at the same time as those at Port St Mary. Their living conditions, however, were considerably different. During the period of the investigation, the beach at Strandhall was frequently exposed to quite severe wave action and was continually being built up in calm weather and eroded down in rough weather. King (1951) showed that, although in an exposed beach the depth of disturbance during storms was unlikely to exceed 20 cms., where wholesale transportation of sand occurred, the beach was likely to be disturbed to a greater depth, particularly in beaches of coarse sand because they usually have greater slopes than those of fine sand. This description fits the conditions at Strandhall during periods of south-westerly strong winds. Such severe and unstable

living conditions adversely affects the lugworms and one very striking difference from the population at Port St Mary is the much greater proportion of small worms present at Strandhall (see Table 1). This may be due to higher mortality or greater emigration among the larger worms.

Fig. 3 shows that in 1950 male spawning at Strandhall occurred at much the same time as at Port St Mary, that is, about the middle of November. Although the presence of spawned males in October and early November suggests that a little male spawning may have occurred before the main one, there is no evidence for a second breeding period other than this autumnal one.

The varying proportions of the female worms at Strandhall are more difficult to assess. The peak months for female worms were May, June and July 1950 when they formed about 40 per cent of the adult worms ; after July, the proportion of female worms declined until early November and December when 10 per cent and 14 per cent, respectively, were females ; in late November, no female worms were collected but the sample was a small one (twenty-two worms). It was not until October that there was a considerable proportion of ripe female worms (24 per cent) which also had large ripe oocytes (20 per cent). Only a few of these ripe female worms were left by early November, none in late November, and it was clear by December that spawning had occurred. It appeared therefore that female spawning at Strandhall took place sometime after October and before December, probably in November. The spawning samples collected in November were less informative than those from Port St Mary because of the paucity of adult worms ; they do however support the above suggestion.

SPAWNING ELSEWHERE IN THE BRITISH ISLES

During 1951 lugworms were obtained from Plymouth and Cullercoats in England, Belfast in Northern Ireland, St Andrews and Millport in Scotland, Aberffraw, Llanfairfechan and Dale Fort in Wales and Port Erin, Port St Mary, Strandhall and Derbyhaven in the Isle of Man (Fig. 1). Weekly samples of twenty-five preserved worms from between mid tide level and low water neaps

TABLE 7

The spawning period of ten populations of *Arenicola marina* during 1951. (The unbracketed figures refer to the dates of the weekly samples ; the bracketed figures to mass spawning of sperm puddles).

SPAWNING IN OCTOBER

Dale Fort : Male and female spawning 19. x.–26. x. Epidemic spawning.

Whitstable : Male spawning (26. x.–27. x). Epidemic spawning.

SPAWNING IN NOVEMBER

*St Andrews : Male spawning 31. x.–7. xi.–13. xi. ; (1. xi.–2. xi. below L.W.N.). Female spawning 31. x.–7. xi. Epidemic spawning.

Plymouth : Male and female spawning 1. xi.–14. xi. The sample between 1. xi.–14. xi. was missed.

Millport : Male and female spawning, 8. xi.–21. xi. The sample between 8. xi.–21. xi. was missed, but spawning probably began soon after 8. xi.

*Port St Mary : Male spawning 12. xi.–17. xi.–22 xi. ; (19. xi.–20. xi.–21. xi). Female spawning 12. xi.–17. xi. Epidemic spawning.

Aberffraw : Male and female spawning 9. xi.–23. xi. The sample of 16. xi. consisted of five worms only and was rejected. During October more than a quarter of the worms had spawned, but on 23. xi a third of the worms were still ripe. Spawning at Aberffraw was therefore a long process lasting several weeks, but most occurred between 9. xi.–23. xi.

*Llanfairfechan : Male and female spawning 13. xi.–23. xi. Female spawning started before 13. xi. but most occurred between 13. xi.–23. xi. Most male spawning took place after 23. xi., but the intervening samples were missed and in the next available samples (19. xii.) most of the males were spent or empty.

SPAWNING IN DECEMBER

*Derbyhaven : Male spawning 6. xii.–10. xii. Female spawning 23. xi.–10. xii. Epidemic spawning.

Belfast : Male and female spawning after 29. xi. On 29. xi, the last sample collected, two-thirds of the worms were still unripe. All the samples from Belfast consisted of large, adult worms. This population spawned much later than the others.

NO SPAWNING DETECTED

Cullercoats : Very few of these worms showed any signs of sexual development during the period of the investigation, probably because they were juvenile worms (31 per cent of the worms were less than 0·5 c.c. and 71 per cent less than 1·0 c.c.). In view of Storrow's (1925) record of spawning in September, it is interesting that the few sexual worms collected in 1951 were in a spent condition as early as September and early October.

Strandhall and Port Erin : Samples from between M.S.L. and L.W.N. collected during November 1951 consisted solely of small immature worms. In 1950 the lugworms at Strandhall and Port Erin spawned sometime in November.

* Localities at which female worms either began or finished spawning earlier than the males.

were sent to me by local workers from each of these localities other than the Isle of Man from mid-September until the end of November or the beginning of December. Two samples of worms were sent from Whitstable in October.

Of the thirteen populations whose spawning periods it was decided to investigate, it was possible to determine the spawning dates of nine only; these are given in Table 7 along with some comments, and Fig. 4 shows the changes in the sexual condition of the worms from some of the populations during the period of the investigation.

It is clear that *Arenicola marina* spawned during the last three months of 1951 but there was considerable variation in the dates of spawning between different populations and each population apparently had its own characteristic breeding period. In five populations (Whitstable, St Andrews, Port St Mary, Dale Fort and Derbyhaven) there is evidence that an epidemic spawning occurred when the great majority of worms voided their germ cells within two or three days ; however at Port St Mary (and at Whitstable, see Newell, 1948) the breeding period was longer than this, sperm puddles having been seen for fourteen days in 1950 and six days in 1951 (Table 4). Spawning started slowly, reached a maximum and then declined in intensity. The advantage of such an epidemic spawning for a sedentary polychaete casting its gametes into the sea are well known (Thorson, 1946) ; the difficulty lies in determining the factors stimulating it. When such factors are identified, it may help to explain the situation at Aberffraw and Llanfairfechan where there is no indication of an epidemic spawning among the lugworms whose breeding lasted over several weekly samples.

Table 7 shows another curious feature of the breeding of *Arenicola*, namely the difference in the time of male and female spawning. It has already been mentioned that in 1950 the female worms at Port St Mary spawned slightly earlier than the males. Table 7 and Fig. 4 show that in 1951 the female worms either began or finished spawning earlier than the males in four populations (St Andrews, Port St Mary, Llanfairfechan and Derbyhaven).

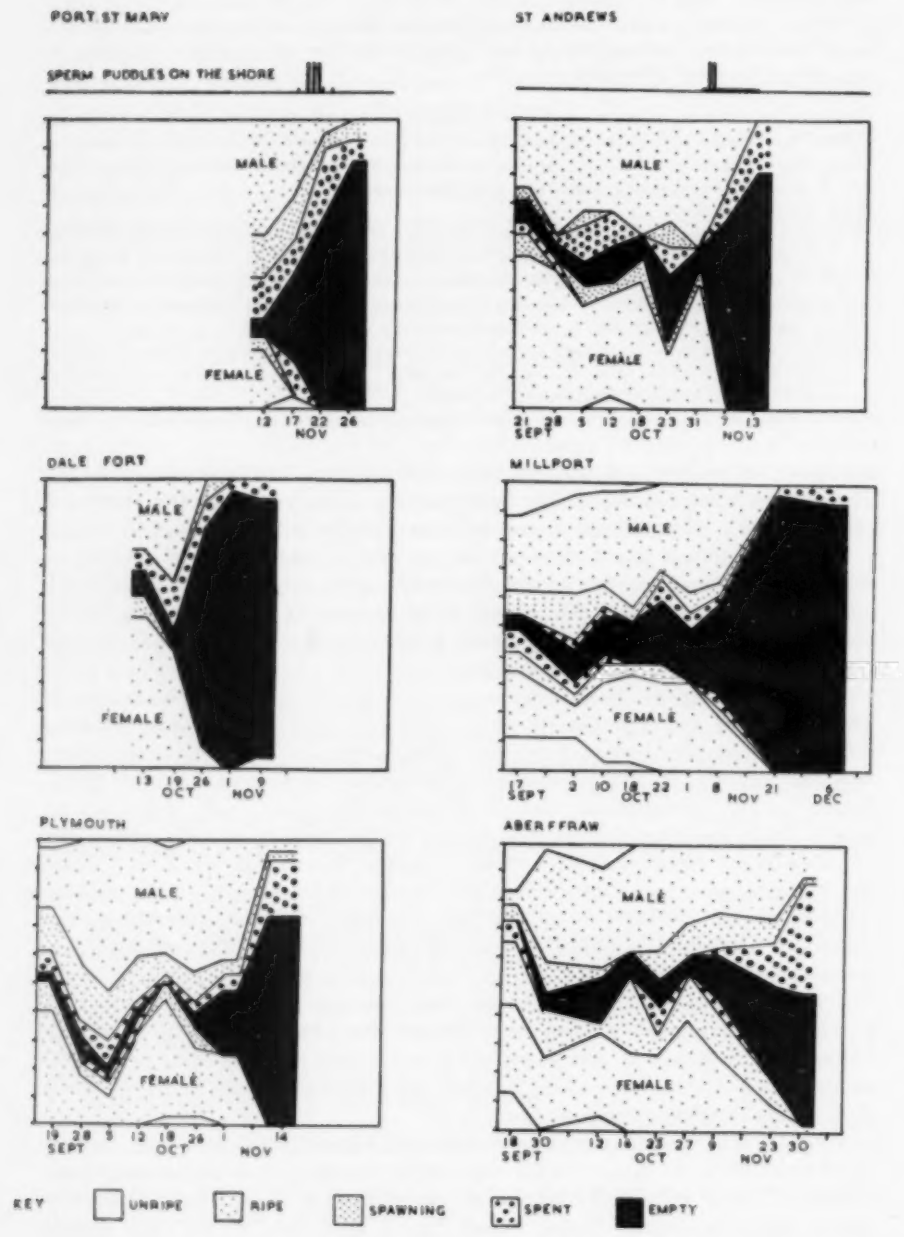

Fig. 4.

[Continued next page]

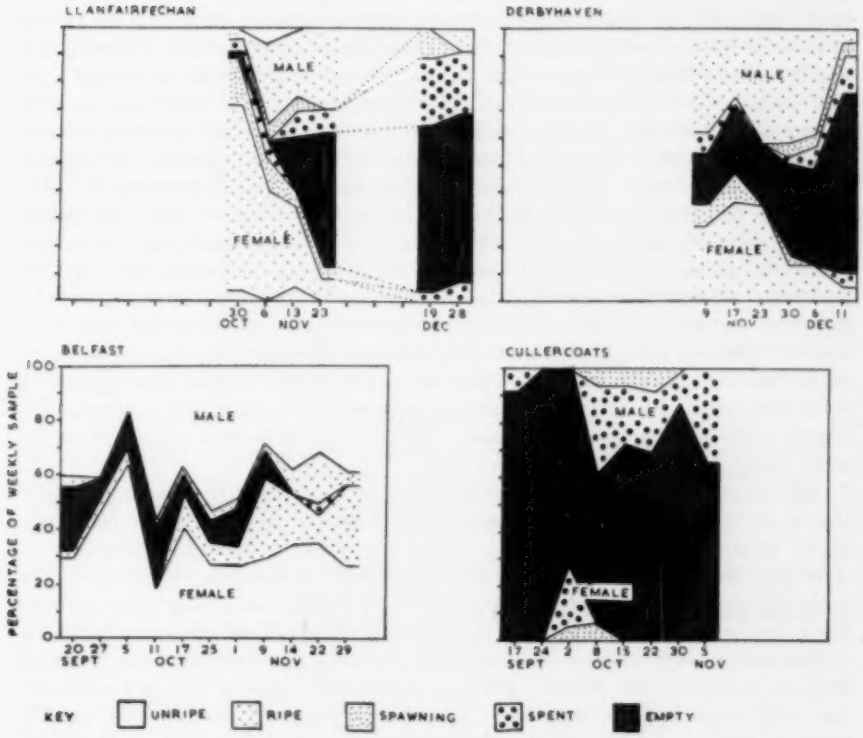

Fig. 4.—Diagram to show changes in the sexual condition of *Arenicola marina* at ten beaches during the breeding season of 1951. The onset and completion of spawning is indicated by the rapid decline in the proportions of male and female worms and the corresponding rapid increase in the proportions of empty worms.

DISCUSSION

The factors influencing the breeding cycle and spawning

The discrepancies in length of spawning and in time of male and female spawning raise several questions. For how long are worms 'spawning' ripe before the main spawning? What factor(s) stimulate spawning? Do the same factor(s) influence male and female spawning? And for how long are eggs viable after spawning?

Howie (1954) found that extracts from the coelomic fluid and gut wall, but not similar extracts from the body wall and nephridia, when injected into lugworms induced the male worms to emit active sperm five to six weeks before the time of shore spawning. None of the injected female worms spawned until much nearer the time of shore spawning when he managed to induce a few females to spawn. He suggests that there are at least two active factors in the extracts, namely, a spawning factor and a ripening factor.

Thorson (1946) discusses the timing of male and female spawning in

marine invertebrates which shed their sexual products into the water ; in many species, the ripe females will not spawn unless induced to do so by swarms of sperms of their own species. He gives many examples from a great variety of phyla and suggests that it must be regarded as an ecological rule that males spawn first thus stimulating the females to shed their eggs in such species as release their sexual products into the sea. However, he does mention that in two polychaetes *Nicolea zostericola* and *Perinereis marionii*, the females may spawn earlier as well as later than the males. As Thorson points out, where an epidemic spawning is the rule, it matters little whether the males induce spawning in females, or either sex is able to induce spawning in the other, the ecological result is the same. In *Arenicola marina* the sexes either spawn at much the same time (as far as can be determined from weekly samples) or there is a tendency for female worms to spawn earlier than the males. There is no information in the literature on how long the eggs remain viable, but some eggs kept for seven hours and twelve hours after spawning were fertilized upon addition of an active sperms uspension and subsequently began to divide in a normal manner. Suspensions of sperms were still active after thirty hours and forty-nine hours.

Okada (1941), working on *Arenicola cristata*, found that the discharge of the sexual products of both sexes was influenced by the presence of the other sex or its sexual products. We may enquire whether it would be possible in *Arenicola marina* for male spawn to stimulate female worms or female spawn male worms. Although both male and female worms can and do spawn under water, as was observed in laboratory tanks, on the shore the epidemic spawning of the males takes place some time after the tide has receded, usually about half an hour after low water. On well drained dry shores, the sperm masses are rarely seen because they have soaked into the sand, but on wet, muddy beaches they are readily visible on the surface where they colour nearby pools white with spermatozoa. Under such conditions of surface standing water and/or when the tide first returns, female worms can irrigate their burrows drawing in a suspension of highly concentrated spermatozoa. It is at this point that the females can be in contact with swarms of sperm and can be stimulated if such a stimulation is a factor inducing female spawning. The scarcity of previous records of spawned eggs of *Arenicola* and the fact that only one egg puddle was ever found at Port St Mary despite frequent and careful hunting from September to December in both 1950 and 1951 suggests that the females do not spawn at low water but when re-covered by the sea. However, crude experiments of adding ' sperm water ' to dishes containing ripe ' milky ' female lugworms showed no more female spawning than did the control worms. If, as seems likely, the reason why few spawned eggs have been seen on the shores where sperm puddles were often found is that females spawn when covered by the sea, then it is difficult to imagine the possibility of concentrations of eggs stimulating male worms in their burrows. It would however be interesting to test the effect of ' egg water ' on ripe male worms, since it does appear that in some populations in 1951 the female worms started spawning before the males.

Orton (1920) states " that most animals under normal conditions begin to

breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely at either the maximum or minimum temperature of the locality " and concludes " that sea temperature must be the influence of paramount importance controlling breeding in marine animals under normal biological conditions ". Thorson (1946) agrees with the former statement but distinguishes between temperature as a factor influencing the ripening of sexual products and temperature as a stimulus to spawning.

Arenicola marina lives in a burrow in sand most of its life. It is there subjected daily to sudden changes in temperature of the sand, due to tidal movements, which at Port St Mary may be as much as 14°C (at 10 cms. depth) in June or as little as 1°C to 2°C in the autumn (see column 5 in Table 8). In addition, it is also subjected to more gradual seasonal changes in temperature ; in summer the air temperature warms the sand during low water whereas it is the sea which increases the sand temperature during the winter months. In the lugworms at Port St Mary, the gonads were most actively proliferating

TABLE 8

Monthly mean values of air, sea and sand temperatures throughout one year (1951) in the south of the Isle of Man. (Air and sea temperature means were obtained from records taken twice daily at Port Erin ; the sand temperature means from records made at least once weekly at Port St Mary).

Months	1 Air	2 Sea	3 Mean Range between air and sea temperatures *	4 Sand Temp. at Ebb Tide			5 Mean Range of sand temperature (Max./Min. thermometer)†
				Surface of sand	10 cms. depth	20 cms. depth	
January	6·0	7·6	−1·7	6·0	6·2	6·7	4·6
February	4·6	6·9	−2·2	5·9	5·7	5·9	4·3
March	5·0	6·7	−1·7	7·5	6·8	6·7	6·3
April	7·4	6·9	+0·3	10·5	9·6	8·6	7·2
May	11·9	7·7	+3·2	10·0	9·5	9·0	10·0
June	15·5	10·3	+5·3	16·7	15·5	14·5	14·2
July	17·7	13·1	+4·7	14·9	14·6	13·9	8·5
August	15·8	13·6	+2·2	17·3	16·8	16·5	3·2
September	14·2	13·4	+0·8	15·5	14·8	14·4	4·4
October	11·6	12·8	−1·2	12·2	12·1	12·2	3·5
November	9·7	12·0	−2·3	9·8	10·2	10·6	1·9
December	7·3	10·8	−3·5	8·2	8·5	8·8	2·5

* The temperature range is given as a minus figure when the air temperature was less than that of the sea, and a positive figure when the reverse was true.

† A maximum-minimum thermometer inside an iron cylinder was buried in the sand, so that the bulbs were 10 cms. below the surface near mean sea level, and was read once a week.

small immature germ cells into the coelom during a period (March to June or July, see Fig. 3) when the worms were being subjected to ever increasing fluctuations in temperature (column 5 of Table 8) ; because the air temperature was rising rapidly (column 1) the sea temperature more slowly (column 2) consequently the difference between the sand and sea temperatures was at its greatest. The increase in size and maturation of these germ cells (from

July to October) took place during much more settled temperature conditions ; the air temperature was declining slowly while the sea temperature continued to rise, consequently the worms had to contend with much slighter fluctuations of sand temperature (column 5). This is a period which must tax the worm's resources severely to provide sufficient nourishment for thousands of developing gametes, so that it is revealing that the growth of the germ cells coincides with a period when the sand temperature (column 4) is the highest for the year and when presumably the metabolism of the worm is most active.

It appears unlikely that *Arenicola* spawns at a definite temperature which is a physiological constant for the species as Newell found that the worms at Whitstable spawned at the same time in 1951 as in other years, although the sand temperature was 5°C lower. Orton's second suggestion, that a period of temperature change can induce spawning, also seems unlikely in *Arenicola* since in the British Isles the species spawns during the three months of the year when the air temperature is still dropping. Moreover, each population has its own characteristic spawning period which is maintained despite temperature variations as was shown by the population at Whitstable which has spawned during the latter half of October for five consecutive years.

The importance of tidal influence in the spawning of polychaetes is well known. Table 9 gives all the known records of authentic male spawning of *Arenicola marina* (as indicated by the presence of sperm puddles on the shore) and shows that peak male spawning is closely associated with neap or spring

TABLE 9

Records of male spawning of *Arenicola marina* (as indicated by the presence of sperm puddles on the shore) in relation to lunar and tidal phases.

Locality	Dates of Peak Male Spawning	Dates of Lunar Phases	Tidal Phases
Cullercoats (Storrow, 1925)	23rd, 24th Sept. 1924	3rd Qtr.: 21st Sept.	Neaps
Belgian coast (Pirlot, 1933)	13th, 14th Oct., 1928	New Moon : 13th Oct.	Springs
Belgian coast (Pirlot, 1933)	14th, 15th Oct. 1932	Full Moon : 14th Oct.	Springs
Belgian coast (Pirlot, 1933)	6th, 7th Oct. 1933	Full Moon : 3rd Oct.	Springs
*St. Andrews (Howie : letter)	24th–26th Oct. 1950	Full Moon : 25th Oct.	Springs
*St Andrews (Howie : letter)	1st, 2nd Nov. 1951	New Moon : 30th Oct.	Springs
†Whitstable (Newell, 1948)	25th, 26th Oct. 1947	1st Qtr.: 22nd Oct.	Neaps
†Whitstable (Newell : letter)	26th, 27th Oct. 1951	3rd Qtr.: 22nd Oct.	Neaps
†Port St Mary (present work)	14th–16th Nov. 1950	1st Qtr.: 16th Nov.	Neaps
†Port St Mary (present work)	19th–21st Nov. 1951	3rd Qtr.: 21st Nov.	Neaps

* Localities at which the sperm puddles were observed below low water neaps.

† Localities at which the sperm puddles were observed in the region between mid-tide level and low water neaps.

tides. Pirlot (1933) and Newell (1948) have shown that the male spawning of *A. marina* on the Belgian coast and at Whitstable respectively coincided with certain phases of the tide ; on the Belgian coast spawning occurred during spring tides in three different years and at Whitstable with neap tides for five consecutive years. An examination of the phases of tides during the 1951 male spawning of nine British populations (Table 10) shows that in every case except one it coincided fairly convincingly with neap tides which occurred on 22nd October, 6th November, 21st November and 5th December.

However, at St Andrews the worms living below low water neaps mark produced the greatest concentrations of sperm puddles on 1st and 2nd November, that is during the spring tides of 30th October, whereas the male worms from above low water neaps mark at this beach spawned about a week later (only a very few sperm puddles were seen but Fig. 4 shows that there were still many

TABLE 10

The male spawning of ten populations of *Arenicola marina* in 1951 in relation to lunar and tidal phases. (The unbracketed figures refer to the dates of weekly samples ; the bracketed figures to mass spawning of sperm puddles).

Locality	Dates of Male Spawning 1951	Dates of Lunar Phases	Tidal Phases
Dale Fort	19th — 26th Oct.	3rd Qtr.: 22nd Oct.	Neaps
Whitstable	(26th, 27th Oct.)	3rd Qtr.: 22nd Oct.	Neaps
St Andrews	31st Oct. to 7th–13th Nov.	1st Qtr.: 6th Nov.	Neaps
St Andrews*	(1st, 2nd Nov.)	New Moon, 30th Oct.	Springs
Plymouth	1st — 14th Nov.	1st Qtr.: 6th Nov.	Neaps
Millport	8th — 21st Nov.	1st Qtr.: 6th Nov.	Neaps
Port St Mary	12th–17th–22nd Nov. (19th, 20th, 21st Nov.)	3rd Qtr.: 21st Nov.	Neaps
Aberffraw	9th — 23rd Nov.	3rd Qtr.: 21st Nov.	Neaps
Llanfairfechan	13th–23rd Nov.+after	? 3rd Qtr.: 21st Nov.	Neaps
Derbyhaven	6th — 10th Dec.	1st Qtr.: 5th Dec.	Neaps

Note : All the lugworms came from between mid-tide level and low water neaps except those from St Andrews* which came from below low water neaps.

ripe males present on 7th November,) and so coincided with the neap tides of 6th November. Therefore there appears to have been two spawnings at St Andrews in 1951, in different parts of the beach, separated by a week or more.

The situation at St Andrews was complicated by the possible presence of two varieties of *Arenicola marina* (Howie). The claim that *A. marina* exists as two varieties was made by Gamble & Ashworth (1898) and Ashworth (1904, 1912). However, Wells (1957) has cast doubt on the characters distinguishing the laminarian variety and suggests that its status requires re-examination. While the status of the low water lugworms is in doubt, it is difficult to assess the significance of the week's difference in the time of male spawning of worms living above and below low water neaps at St Andrews which occurred in 1950 and 1951. At Port St Mary, worms living below low water neaps (and collected during spring tides) quite clearly spawned at the same time as the rest of the population, that is during neap tides.

The close coincidence of breeding with tidal phases indicates that some external factor(s) associated with tides are responsible for the release of the germ cells. The suggestion of Korringa (1947) that in regions of considerable tidal range the regular rhythmical differences in water pressure act as a spawning stimulus is more convincing for a species which spawns at regular intervals throughout a fairly long breeding season than for *A. marina* which breeds only once a year for a very short period after a long period of maturation. However, it is conceivable that such a factor (in the case of *Arenicola* it would be the gradually decreasing water pressure of neap tides) could stimulate animals brought to such a state of ripeness that any changing factor could induce

spawning. It is interesting that in 1950 a few males spawned at Port St Mary during the early November neap tides although the epidemic spawning took place during the later neaps (Table 4), and that slight male and female spawning occurred before the main spawning in several populations investigated in 1951 (Fig. 4). Seasonal temperatures are probably important in establishing the breeding seasons, during which Howie's ripening factor is at work. Once the animals are in a state of ' spawning ripeness ', when they are in a condition of extreme turgidity, changes in water pressure may act as a physical stimulus.

Throughout the discussion we have been confronted with possibilities rather than conclusions, and it may seem premature to enquire into the reasons for the differences in spawning time between various lugworm populations. It may however be pointed out in conclusion that whole responsibility need not rest on the environment, for the comparatively sedentary habits of lugworms living in a discontinuously distributed habitat would favour local genetic differentiation. That this actually occurs is suggested by the fact that local populations may differ, not only in spawning time but in other characters too : this question has been discussed elsewhere (Wells, 1957, Duncan 1959).

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SUMMARY

The breeding of *Arenicola marina* from two beaches in the Isle of Man, one exposed to and the other sheltered from wave action, was studied. Both populations spawned only once during the year, in autumn, after an extended period of sexual development. The population living in exposed conditions had a higher proportion of juvenile non-breeding worms than the sheltered populations, due to loss of adult worms (by mortality and/or migration) resulting from unstable environmental conditions. Lugworms from the Isle of Man are capable of becoming sexually mature for the first time in their second year of life and at a size of between 0·5 c.c. and 0·9 c.c. (about 2 to 3 cms. chaetigerous length).

Male spawning in 1950 and 1951, detected by the occurrence of sperm puddles on the surface of the sand, occurred mainly during three days at the later November neap tides, but some slight spawning also took place before and after. Female spawning could only be detected by examination of the coelomic contents and it appeared that during both years the male and female spawning was not simultaneous, there being a few days difference in the start and finish of the process.

In 1951 spawning occurred in nine populations of British lugworms during the neap tides of October, November and December. In all nine populations the male spawning coincided with one of these neap tides, but at St Andrews worms from below low water neaps spawned during spring tides. In four populations the female worms apparently began or finished spawning slightly earlier than the males. In five populations, spawning was epidemic but in two it extended over a period of several weeks.

Possible factors inducing spawning are discussed.

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ADDENDUM

Howie (1959, *J. mar. biol. Ass. U.K.* **38** : 395) records for several years the spawning dates of populations of *Arenicola marina* from St Andrews and from Booterstown and Seapoint, near Dublin. The peak spawning of the two Dublin populations (detected by a drop in the proportion of worms with genital products) coincided with neap tides as in most other populations, but the worms from Booterstown, collected from above L.W.N.T., spawned in the middle of November during 1954, 1955 and 1957, whereas the worms from Seapoint, collected from below L.W.N.T., seem to have spawned during the preceding neaps in the years investigated. At St Andrews, however, peak

spawning was seen to occur on the shore during the spring tides of the latter half of October for three consecutive years (1950–52), and possibly also in 1949 ; Howie does not mention any difference in the time of spawning of worms from above and below L.W.N.T. The breeding season at St Andrews and Dublin was preceded by, or coincided with, the first sharp fall in air temperatures during low tide, which Howie suggests, provided the spawning stimulus. He also reports a spring spawning (detected by a drop in the proportion of worms with genital products) in 1958 among worms with ' littoral ' characteristics from below L.W.N.T. at Fairlie Sands, Millport.

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